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THE ANATOMY OF THE NORTH AMERICAN
CONIFERALES TOGETHER WITH CERTAIN
EXOTIC SPECIES FROM JAPAN AND
AUSTRALASIA. PART I.

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INTRODUCTORY.

THE present work had its origin in 1880, in an attempt to construct a system of classification for the North American Coniferae, based upon the anatomy of the vascular cylinder of the mature stem. The fundamental idea was that such a classification would prove of great value in the identification of material used for structural purposes, but investigations had not been carried very far when it became manifest that some such arrangement was imperatively demanded in other directions and for purposes of a more strictly scientific character. In entering upon the study of fossil plants it was recognized that the most fruitful source of reliable data must be found in the stem structure. At that time there was little in the way of an adequate basis for further study of this sort, inasmuch as the current diagnoses of the vascular structure were found in most cases to be singularly inadequate, and often so incorrect as to require exten-

sive revisions. It was furthermore found that, in order to reach correct conclusions in the case of stems which must often present marked structural alterations arising through the influence of decay and other conditions attending fossilization in its various forms, it was indispensable that there should be a trustworthy means of comparison with existing types, whereby sources of error arising from eliminated structures might be definitely excluded, and the fossil referred with certainty to its nearest relative. The original intention was therefore modified with a view to meeting the requirements of palæobotanical research. During the twenty odd years these investigations have been in progress, there has been much change in the views held by botanists respecting the significance of anatomical features as affording evidence of descent, and our own studies brought forth facts which gave repeated emphasis of the most positive kind, to the idea that questions of phylogeny cannot be settled either by the morphologist in the narrower sense or the physiologist, either separately or combined, and that a proper historical point of view can be gained only when to such labors we join the data derived from a critical study of the stem structure in all its details. As the greater may always be held to include the less, the present discussion is to be regarded primarily from the biological point of view, and questions of descent will take precedence over those of mere taxonomy.

The original intention was to make a complete study of all the North American woods, comprising, as enumerated by Sargent in his report in the *Tenth Census of the United States*, some four hundred and nineteen species and varieties; but the great importance of the Coniferæ from an economic point of view, their frequent representation in the fossil state and their relatively more simple structure, eventually led to their selection as the one group in which initial studies might be prosecuted with the most immediate and profitable results. While the North American species constituted the original basis, various exotic species were added from time to time with the result that our studies as now completed, comprise ninety-two species from North America, twenty-one species from Japan, and four species from Australasia. This extension has proved of great value, not only from a

palæontological point of view, but also because of the important bearing such exotic types have had in the solution of questions relating to descent. The methods adopted in these investigations have already been fully explained (38, p. 33 *et seq.*) and further details at this time are uncalled for.

In 1896 the work had reached such a point that it was deemed desirable to make a preliminary statement of results. This appeared in a paper published in the *Transactions of the Royal Society of Canada* entitled the "Generic Characters of the North American Taxaceæ and Coniferæ," in which it was shown that generic differentiations were possible. The diagnoses and artificial key to the genera thus published, have been in constant use since that time for the determination of fossil species, with the most gratifying results; and after seven years of severe testing, and in the light of more extended studies, they are found to be substantially correct and reliable.

The question of specific differentiation presented a far more difficult problem, the solution of which has now been reached as embodied in the present work.

In the prosecution of these studies I have been under deep and often constant obligations to helpful friends working along other lines. To Prof. C. S. Sargent of the Arnold Arboretum, as also to Mr. Morris K. Jesup, President of the American Museum of Natural History; Dr. N. L. Britton, Director of the New York Botanical Gardens; the late Baron Ferd. von Mueller of Melbourne, Australia; Sir W. T. Thistleton-Dyer, Director of the Royal Gardens, Kew; and to Mr. E. J. Maxwell of Montreal I am indebted for much valuable type material. To Dr. B. E. Fernow, formerly Chief of the Bureau of Forestry of the United States Department of Agriculture, I am under obligations for a large amount of material specially selected with reference to testing the accuracy of diagnoses and details of the key. To Mr. J. G. Jack of the Arnold Arboretum, I am under particular obligations for the readiness with which he has frequently responded to requests for material of a trustworthy character, and his care in selecting a large series of specimens for testing purposes, which have contributed very largely to the success of the final results. To my assistant,

Miss C. M. Derick, I wish to extend my appreciation of the frequent and valuable assistance she has rendered.

SPIRAL TRACHEIDS.

In the genesis of the vascular system, the elements first differentiated from the generative tissue, constitute the primitive elements now generally recognized in accordance with the designation of Rusow as protoxylem. These elements are tracheids, and in the Coniferales as also in the Ginkgoales, they always occupy a position immediately external to the pith and therefore on the inner face of the zone representing the growth of the first year, but they are not repeated in the formation of xylem structure in subsequent years. The primitive character of such tracheids is therefore indicated, not only by their position and relation to development of other parts, but it is also exhibited by their occurrence in plants where the vascular system is of a far more simplified type and of which they constitute relatively more prominent features. In the Equisetineae, both fossil and recent, they are conspicuous elements of the vascular structure, being found within the limits of the carinal canal. They similarly occur in the Ophioglossaceae and elsewhere among the more primitive of the vascular plants. The general evidence, then, which may be derived from a comparative study of various types, tends to enforce the idea that, originating as a primitive form of the wood structure, and more or less common to all the vascular plants, they are relatively predominant in the lower forms, with a tendency to obliteration through replacement or modification in the higher types, where their presence may be held to represent a survival of ancestral characters. This view gains additional support from a study of the peculiar structural variations which characterize such tracheids, and the progressive modifications which they have been found to undergo in relation to the development of the secondary xylem.

The protoxylem elements are distinguished by the presence of thin, spiral bands disposed upon the inner surface of the primary wall in such a manner as to afford a substantial measure of mechanical support. These ribbon-like bands represent second-

ary growth in thickness of a local nature—the localization being determined with reference to the requirements of such support in the first instance. De Bary (9, p. 57) has shown that they exhibit considerable variety in the number of fibres and the direction and steepness of the coils. Their number is often only 1–2 in narrow tubes which are first formed when the differentiation of tissues begins, in others 4 or more, and it rises in many cases in the angiosperms to 16–20. He has furthermore pointed out that the steepness of the coils is greatest in those tubes which are developed earliest, before the extension of the part to which they belong has ceased; since in these the coils are separated from one another by the extension which the tube itself undergoes. These facts appear to suggest that the more typical the spiral tracheid is, the more fully does it emphasize the idea of a primitive structure; but that as the spirals become more dense or closer, there is a tendency toward more uniform and less localized secondary growth of the wall, as expressed in the structure of the higher types of plants or the secondary xylem elements of the Coniferae. In confirmation of such a view, reference may be made to the commonly observed fact that the spirals tend to a more compact arrangement at the ends of the elements, becoming correspondingly more open in the central region; and likewise to the well known transitional forms which these structures exhibit, whereby their original characteristics are completely lost as they merge ultimately into tracheids devoid of spirals, but characterized by the presence of pits of various forms. In 1840, Don (52) pointed out that the tracheids of *Cycas revoluta* exhibit scalariform structure at one end and bordered pits at the other. This fact has more recently been commented upon by Williamson who observed the same fact independently, and drew from it the inference that a definite relation exists between the scalariform markings and the pit structures of such a nature that the one is the natural successor of the other. In *Ginkgo biloba* which is now generally conceded to represent a much more primitive type than the Coniferae, though more advanced than the cycads, precisely similar transformations are to be met with. The evidence of fossil plants is quite as convincing as that derived from existing



FIG. 1.



FIG. 2.



FIG. 4.

FIGS. 1-4.—*Cordaites brandlingii*. Radial series showing the origin of bordered pits from spiral tracheids. $\times 180$.

species, while it is often of distinctly greater value because affording data derived from presumably more primitive types. Thus such transitions are well known, though of a relatively simplified form in the structure of the calamitean stem, and an excellent example of this kind is afforded by a figure given by Scott (43, p. 22). In 1869 Williamson (52, p. 69) directed attention to the occurrence of such transformations in the tracheids of *Cordaitea* (*Dadoxylon*). A more recent study of this genus (39, p. 57 and 43, p. 418) has shown that this feature is well exhibited in *C. brandlingii*, where a suitable radial section (Figs. 1-4) will present a more or less graduated series of transitions from the typical spiral tracheid of the protoxylem, through scalariform structures to the multiseriate bordered pits of the tracheids in the secondary xylem; while within the limits of the same tracheid, such transitions may be observed as it were, in process of development, affording the most conclusive proof in this respect. These transitions as observed in *Cordaitea brandlingii* show the following phases:

In the successive radial development of new tracheids, there is a constant tendency to a more uniform thickening of the cell wall by secondary growth. This at first finds expression in the more compact arrangement of the spirals which later coalesce at various points, thus giving rise to more localized areas devoid of secondary growth, and hence to a scalariform structure in which the general lines conform more or less exactly, to the direction of the original spirals. By a further modification the elongated, thin areas become converted into shorter, often isodiametric areas substantially by a process of division. A further tendency to general thickening of the walls causes the margins of the scalariform structure to project from all sides and extend over the area of arrested growth as a lip which never completely closes at the centre, where there is left a usually circular, sometimes oval or again lenticular or even oblong opening, and in this manner the bordered pit is formed.

The region within which these changes occur, or the "transition zone," is subject to great variation whereby the change from spiral to bordered pit may arise very gradually through a broad radial zone, as in *Cordaitea brandlingii* or it may occur very

abruptly as in the modern *Coniferæ*. The general tendency of such evidence is to show that with a higher type of organization, there is a corresponding diminution in the transition zone and increased abruptness in the structural alterations. The logical result of an extension of this process would be the reduction of the bordered pit to the condition of a simple pit, and ultimately, its complete obliteration. In the *Coniferæ* the reduction of the bordered pit to the condition of a simple pit sometimes occurs in the case of medullary rays or even in the case of tracheids with very thick walls, but it becomes most prominent in the angiosperms where it is a characteristic feature. Instances also occur in some of the hard pines, in which the pit is completely obliterated. This applies in particular to tracheids of the summer wood, the walls of which have become unusually thickened.

The relations to which attention has thus been directed somewhat in detail, have been expressed in more general terms by De Bary (9, p. 321) in the statement that "Outside the primitive elements, wider trachæ follow. Their development takes place successively, advancing from the inner edge of the bundle outwards, and as a rule at a time when the elongation of the entire part to which they belong is nearly at an end. The thickenings on their walls therefore have a successively denser arrangement: dense spiral and annular trachæ, then reticulated and pitted trachæ follow one another in succession from within outwards, with gradual transitions, or with the omission of one or the other immediate form." It is probably a justifiable inference from the preceding facts that, the relation which exists between the spiral tracheids of the protoxylem and the pitted tracheids of the secondary xylem in the *Coniferæ*, is, in general terms and from the standpoint of development, the same as that exhibited between the lower and higher types of vascular plants.

Accepting the general principle which appears to be justified by the foregoing facts, that the transition from spirals to bordered pits is a feature in development which bears a direct relation to the evolution of higher types of organization, we may utilize it for the purpose of determining the general phylogeny of the *Coniferæ* so far as they may show a survival of such characters. Out of a total of 117 investigated species of indigenous

and exotic Coniferæ, 9.4 % show a more or less permanent survival of the spiral structure within the limits of the secondary xylem. Of these 6 % fall within the Taxaceæ (*Torreya* 3.45 %, *Taxus* 2.5 %), while in the Coniferæ the remainder is divided between *Pseudotsuga* (1.7 %), *Larix* (0.86 %) and *Pinus* (0.86 %). In the genus *Torreya* the spirals are, on the whole, rather open and distinguished by being 2-4 seriate. They are typical throughout the spring wood, but in the thin summer wood they quickly become vestigial and ultimately disappear altogether. In *T. taxifolia* there is also a marked condensation whereby the spirals are all brought into a more compact series within the earlier tracheids of the summer wood. All of these changes appear to be directly related to a progressive increase in the thickness of the tracheid wall.

In all investigated species of *Torreya*, there is a rather wide variation in the angle which the spirals make with the axis of growth, and this becomes most pronounced in *T. californica*, which gives the lowest angle for any species of either *Torreya* or *Taxus*. Usually the spiral has an angle quite distinct from that of the lines of striation in the cell wall, but in *T. taxifolia* the two often coincide. The following will show the various details derived from the average of ten measurements for each species.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.
<i>Torreya nucifera</i>	70.5	87.0	57.0	30.0
" <i>taxifolia</i>	70.4	77.0	61.0	16.0
" <i>californica</i>	46.2	63.0	30.0	33.0
Means	62.3	75.7	49.3	26.3

In the genus *Taxus*, the spirals are rather close and in 2, rarely 3 series. As in *Torreya* they are typical throughout the spring wood, and show a pronounced tendency to obliteration in the summer wood. This tendency is subject to considerable variation in different species. In *T. canadensis* the spirals are conspicuous throughout. In *T. floridana* they usually disappear

in the later growth and are wholly wanting in the two or three, last formed tracheids. In *T. brevifolia* they become very imperfect in the outer summer wood and tend to disappear completely, only vestiges remaining in the last formed tracheids. In *T. cuspidata* the spirals are generally absent from the summer wood, or when present, they are merely vestigial. The angle is somewhat greater—about 7 deg.—than in *Torreya*, and this fact is apparent with respect to certain species without special measurement. The four species appear to be paired off in such a way as to represent a mean difference of about 10.9 deg. as between *T. canadensis* and *T. floridana* on the one hand, *T. brevifolia* and *T. cuspidata* on the other. In all cases the angles of the spirals are quite distinct from those of the lines of striation. The following details are based upon the average of ten determinations.

	Average angle.	Highest angle.	Lowest angle.	Extreme range.	Mean of 2
<i>Taxus canadensis</i> . . .	72.4	88.0	66.0	22.0	75.4
" <i>floridana</i> . . .	78.4	90.0	72.0	18.0	
" <i>brevifolia</i> . . .	63.0	76.0	55.0	21.0	
" <i>cuspidata</i> . . .	66.1	87.0	45.0	42.0	64.5
Means . . .	69.9	85.2	59.5	25.7	

A comparison of these results in detail emphasizes the fact that the distribution of the spirals, as between spring and summer wood, is in direct harmony with the principles already stated, and furthermore, that the angles at which the spirals develop do not afford an adequate basis for generic differentiation. It is nevertheless possible to recognize sub-generic groups in such wise that in both genera a general line of division may be established at 70 degrees. In the case of *Torreya californica*, the very low angle of 46.2 degrees may be regarded as a differential character of specific value.

In the genus *Pseudotsuga*, spirals are confined to the tracheids of the spring wood. This has a partial exception in *P. macrocarpa*, in which vestigial spirals may be observed in the earlier tracheids of the summer wood. In this species the mean

angle is 70 degrees, but the spirals are always characterized by lack of prominence, they are often widely distant, and the somewhat extended areas within which they are wholly wanting or fragmentary, suggests a process of obliteration. In *P. douglassi* the average angle is 82 degrees; the spirals are characterized by considerable prominence and they are also, on the whole, close. In this genus these two factors obviously possess a well defined differential value with respect to the two species.

Among the higher genera only two cases are known in which spirals occur, but in each the character is of a very sporadic nature. In *Larix americana* spirals are frequently found in the summer wood, but they are so inconstant in their occurrence, and they present such varying aspects, that the angle cannot be determined. In *Pinus taeda*, where the walls of the summer tracheids are very thick, rudiments of spirals may sometimes be seen. Here also it is manifestly impossible to determine the angle.

Viewing these five genera collectively, their spirals conform fully, in their occurrence and relation to progressive development, to the general principles already stated, and especially as formulated by De Bary. They possess no differential value of generic rank with respect to *Pinus* and *Larix*, but they do have such value with respect to *Torreya* and *Taxus* on the one hand, and *Pseudotsuga* on the other, the differentiation resting upon their occurrence in the summer wood in the former, and their exclusion from that region in the latter. Were any question to arise in this connection, it could be authoritatively decided by the definite association of resin passages and fusiform rays in *Pseudotsuga*.

It only remains for us to ascertain how far such structural features may be employed as a basis upon which to determine the general phylogeny of the genera. As between *Torreya* and *Taxus* there is very little upon which to base conclusions respecting sequence in development, and it is apparent that both of these genera have attained to nearly the same level. Such differences as do exist, however, seem to point to the relatively, though slightly, inferior position of *Torreya* as indicated by (1) the smaller angle in that genus and (2) the generally more com-

pact spirals of *Taxus*. This fact, so far as it possesses phylogenetic value, appears to confirm the conclusions as to the relative positions of these two genera, already determined upon the basis of external morphology as stated by Eichler (11, p. 108).

It has already been made clear from the preceding facts, as well as from former discussions (40, p. 56) that in the case of the *Taxaceæ* and also of *Pseudotsuga*, the spirals must be regarded as a survival of primitive structures. On a former occasion (40, p. 57) I was inclined to consider that their occurrence in *Larix* and *Pinus tæda* was atavistic, but in the light of more recent evidence as now set forth, this opinion requires modification in so far as to include the idea that they do not express mere parallelisms in development, but that they afford evidence of a common ancestral type at some point far anterior to the evolution of the *Taxaceæ*. We must therefore consider that *Torreya*, *Taxus*, *Pseudotsuga*, *Larix* and *Pinus* represent different branches of a general phylum — undoubtedly including also, other closely related genera in which the spirals have been wholly obliterated — which had its origin at a point anterior even to such types as *Cordaitea*, and therefore, in all probability in what Coulter (7) has very happily designated as "the great Cordaitean plexus" arising from the eusporangiate ferns, or what, according to our more recent knowledge, and Coulter's more recently expressed view (8, p. 172) would be designated as the *Cycadofilices*.

BORDERED PITS DISTRIBUTION AND STRUCTURE.

In the preceding pages, the derivation of the bordered pit from the spiral tracheid, and its obviously more intimate relation to a higher type of development have been made clear. Our present purpose is to discuss these structures with special reference to (1) occurrence, (2) distribution, (3) structural modifications, (4) taxonomic value and (5) their value as evidences of descent.

At the outset, reference may be made to the occurrence of bordered pits on the radial walls of the ray cells as exhibited typically in *Sequoia* and *Taxodium*. Their location in such situa-

tions, as also upon the radial, terminal, upper and lower walls of the ray tracheids may be held to represent a feature somewhat distinct from their presence on the walls of the wood tracheids, and their consideration properly belongs to a discussion of the medullary ray as a whole; but it may be observed that they constitute a characteristic feature in the structure of the ray elements in the great majority of the Coniferales.

The occurrence of bordered pits on the walls—especially the radial walls—of the wood tracheids in the Ginkgoales and Coniferales, is much too familiar a fact to call for special discussion at this time, but reference may be made to the additional fact that their characteristic structure is such as to permit of their use for the general purpose of tracing possible lines of descent through such extinct types as Cordaites and the Cycadofilices. It is true that similar bordered pits originating in modifications of spiral structures, are to be met with, often in great numbers, in the higher angiosperms, but in such cases the associated structures permit of a clear and definite differentiation of all such woods from the Coniferales.

Radial walls.—The characteristic situation of the bordered pits is on the radial walls where, as was shown many years since by De Bary (9, p. 160), "the pits of contiguous tracheids always correspond to one another in such a way that on each limiting surface, all the cavities of the pits of one fit exactly over those of the other. The plano-convex cavities are thus applied to one another in pairs so as to form the lens-shaped pit cavities" as seen in tangential section. But on surfaces abutting on elements of another order, *e. g.*, parenchyma cells, the bordered pits of the tracheids correspond to non-bordered pits, or they are opposite an unpitted wall. Four typical variations of the bordered pits may be recognized:—(1) the multiseriate, when they are disposed in any number of rows more than two, (2) the 2-seriate, (3) the uni-seriate with occasional pairs of pits, and (4) the strictly uni-seriate. The general sequence thus presented will be found to be in direct accord with the evolution of higher types of structure and organization.

The most primitive type of gymnosperm presenting a multi-seriate arrangement, is the genus Cordaites. Among eleven

species of this genus which have been critically studied within recent years (39) there is a general agreement in the constancy of this character which thereby becomes of generic value. In all the species the pits are disposed in such a compact manner throughout the entire extent of the tracheid, as to present a hexagonal outline. In *Cordaites acadianum*, they are 2-5-seriate (Fig. 5). In other species they vary from 2-seriate in *C. hamiltonense* and *C. newberryi* (Fig. 6) to occasionally 4-seriate in *C. clarkei*. In the majority of species, the rows are not constant, but show a varying number from 1 to 3, or 2 to 5, this variation

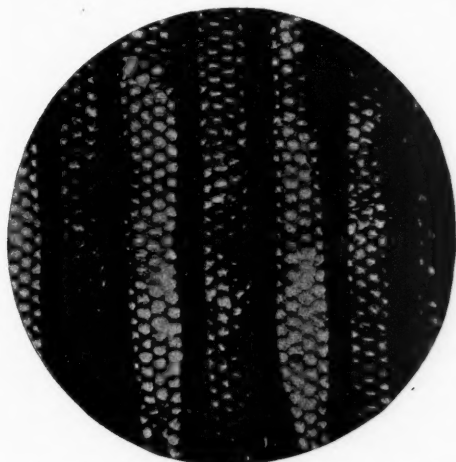


FIG. 5.—*Cordaites acadianum*. Radial section showing disposition of the bordered pits. $\times 180$.

being exhibited by adjacent tracheids in accordance with the variation of the latter in radial diameter; and viewing this distribution as a whole, it cannot be doubted that it represents corresponding differences in development. One of the most striking features of the genus is to be met with in *C. newberryi* (Fig. 6), which is unique in the segregation of the pits into groups of 6-13.

In *Araucarioxylon* Knowlton has shown (25, p. 614) that, while conforming to the characteristic form and compact arrangement presented in *Cordaites*, the pits exhibit far less constancy in their serial arrangement, and in this respect they are at once

comparable with those of the existing Araucarias. Among the latter, *A. cunninghamii* shows a 1-3-seriate disposition; *A. excelsa* is 1-2-seriate while *A. bidwillii* is strictly 1-seriate. All



FIG. 6.—*Cordaites newberryi*. Radial section showing disposition of the bordered pits. $\times 180$.

of the extinct species as comprised in the genus *Araucarioxylon* not only show similar variations, but such variations are found to cover a much wider range. A comparison of all the species, both recent and extinct, now available for that purpose, is of interest in this connection.

	1-ser.	2-ser.	3-ser.	4-ser.
<i>A. bidwillii</i>	X			
<i>wuerttembergianum</i>	X			
<i>schmidianum</i>	X			
<i>hugelianum</i>	X			
<i>excelsa</i>		X		
<i>arizonicum</i>		X		
<i>edvardianum</i>		X		
<i>virginianum</i>		X		
<i>doeringii</i>		X		
<i>subtile</i>		X		
<i>argilliacola</i>			X	
<i>heerii</i>			X	
<i>cunninghamii</i>			X	
<i>robertianum</i>				X

Such a comparison brings into strong relief the fact that the Araucarias, both past and present, constitute a transitional group with a somewhat wide range of variations, and in this respect they may be said to stand between the more stable Cordaites and Agathis on the one hand, and the far more variable Coniferæ on the other, since in *Agathis australis* we find essentially the same features of structure and distribution as in Cord-

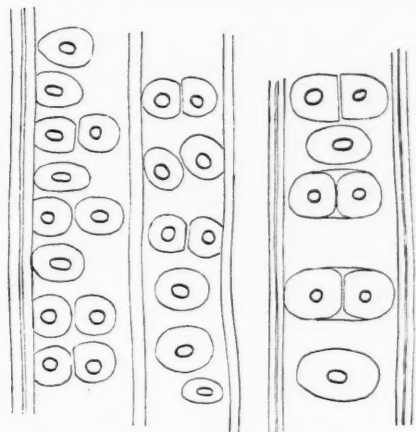


FIG. 7.—*Pinus cubensis*. Radial section showing the form and disposition of the bordered pits. \times 280.

aites, the pits being 1-3-seriate. The sequence presented above may be held to be in the inverse order of development, and *A. robertianum* must therefore be held to represent the most primitive form.

It is apparent that in Cordaites, Araucaria (including Araucarioxylon) and Agathis, the pits are invariably distinguished by two constant features; (1) their hexagonal form and (2) their very compact disposition throughout the entire extent of the tracheid. They often deviate from the multiseriate arrangement typical of the group as a whole, in that in individual cases they are reduced to a 1-seriate arrangement. They thus tend to overlap the next group which is distinguished by a 2-seriate disposition, but any confusion which might arise from this cause, may be overcome by reference to the special form and dis-

position of the pits as will more fully appear in the following lines.

Among the remaining Coniferales, 20 species of various genera, or 17.2 % in all, show a 2-seriate arrangement, and to this group we must also add the Ginkgoales and various fossil species. Here the multiseriate disposition of the pits involves features which at once distinguish the group as a whole from the preceding, clearly placing it upon a higher plane of development. The pits are never hexagonal but generally elliptical or round, while they also show a strong tendency to extreme segregation. When brought into a compact arrangement as in *Cupressoxylon*, *Sequoia* or various species of *Pinus*, they are flattened only along the lines of limited contact, which are usually confined to one end (Fig. 7). A very characteristic feature of this group is the further fact that the 2-seriate arrangement is not constant, either in the same section or in the same tracheid. Both *Pinus tæda* and *P. cubensis*, as also *Larix americana* and *Tsuga canadensis* afford illustrations that while typically 2-seriate, a given section may show a strictly 1-seriate arrangement, and this difference also obtains as between contiguous cells. In all such cases examination will show that the variation is directly related to the relative size of the tracheids in such a way that the narrower tracheids, or those arising from a less vigorous growth, are 1-seriate. Within the individual tracheid there is a strong tendency to a 1-seriate arrangement in the central region, while it is 2-seriate at the extremities; and this law holds so true that in those species which are exceptionally 2-seriate, judgment should be reserved until it is seen that the 1-seriate form holds throughout.

The antithesis of the multiseriate type is found in the 1-seriate form. This is typical of 50 % of all the species included in the present studies. In such cases the form of the pit is never hexagonal or specially flattened. When the disposition is somewhat compact, as in *Pinus strobus* (Fig. 8), the outline becomes more or less strongly elliptical, but as the segregation is more pronounced, a definitely circular form prevails (Fig. 9). Within the limits of the individual tracheid the same law of distribution obtains as in the 2-seriate type, whereby segregation is always most pronounced in the central region.

Between species of the strictly 1-seriate, and those of the strictly 2-seriate type, there is an intermediate or transition group comprising 34 species, or 29.3 % of the investigated species, into which members of the first two groups may occasionally be projected. The distinguishing feature of this group is the occurrence of pits in pairs which are usually distant, and in no case so numerous as to distinguish a 2-seriate disposition. They give undoubted proof of the passage from one type to the other. Like the 2-seriate type, this feature is not confined to any one genus or to any particular group of genera, but it applies with equal force to any genus, the members of which may therefore represent any or all of the three types here specified.

Viewing the distribution of the bordered pits from the standpoint of zonal development, it is found to be universally true that, in the earlier spring wood there

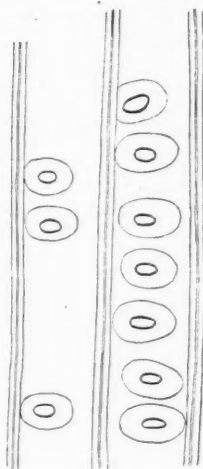


FIG. 8.—*Pinus strobus*. Radial section showing the form and disposition of the bordered pits. $\times 280$.

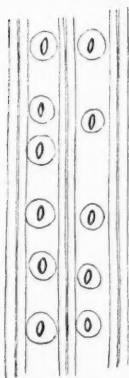


FIG. 9.—*Pinus strobus*. Radial section showing the bordered pits of the summer wood. $\times 280$.

is the strongest tendency to a multiseriate arrangement. With a radial increase of the xylem, this tendency constantly diminishes, with the general result that the pits become more strictly uniseriate and more distant toward the summer wood in which they are sometimes wholly obliterated—this being the case when the cell wall acquires unusual thickness.

Upon careful examination, the foregoing facts will be found to be in exact accord with the law formulated by De Bary with reference to variations in the structure of spiral tracheids and the genesis of bordered pits as already stated. In accordance with this law it is possible to conclude that relatively rapid growth is coordinated with a primitive development, while the converse

is true of a slow rate of growth which is again convertible into terms of maturity. On this basis we may present the following general outline of sequence in development, as preliminary to further and more detailed discussion of phylogeny.

Cordaitea.	2-5	seriate, hexagonal pits.	} Compact throughout the tracheid.
Araucarioxylon.	1-4	" " "	
Araucaria.	1-3	" " "	
Agathis.	1-3	" " "	
Ginkgo.	1-2	" round or oval pits.	} More or less, often strongly segregated.
Higher Coniferales.	1-2	" " " "	
" "	1-ser. & pairs	" " " "	
" "	1-seriate.	" " " "	

Tangential Walls.—The occurrence of bordered pits on the tangential walls is a well-known and characteristic feature of the Coniferales. In the case of fossil forms, to which Araucarioxylon

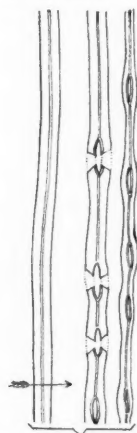


FIG 10.—*Sequoia gigantea*. Radial section showing the bordered pits on the tangential walls of the summer wood. $\times 280$.

offers a partial exception, it cannot be satisfactorily demonstrated because of the peculiar alterations of the cell wall, but that it is present we are permitted to infer from analogy with existing species upon which dependence must be placed for an elucidation of the general law. The typical position for such pits is upon the tangential walls of the summer wood, where they are most satisfactorily seen in radial section, inasmuch as they are always readily observable when present, and their most essential features are displayed in a manner not possible in a tangential section (Fig. 10). Pits occur in this position in 71.7 % of all the investigated species, and their absence in 28.3 % points to some special features in development which may be assumed to have a general bearing upon the question of descent and relationship. In *Agathis*, as represented by the one species, *A. australis*, such pits are a prominent and characteristic

feature, but in the nearly related *Araucaria*, they are remarkable for their uniform absence. In the primitive Ginkgoales they

are also present, but among the Taxaceæ, while generally present, they are occasionally wanting as in *Torreya taxifolia* and *T. nucifera* or 66.6 % of the investigated species of that genus. Nowhere else among the Coniferales do we find such a feature until we reach the genus *Pinus*, the second and higher section of which is invariably characterized by their absence, thus presenting an exceptional feature to the extent of 68.3 % of that genus. That such absence represents a process of obliteration conformable to De Bary's law cannot be doubted, while the sporadic recurrence of this feature in often widely separated genera, or in particular species of a given genus, must be held to have a more or less direct bearing upon the general course of development. This is emphasized by the observation that in *Larix americana* and *L. leptolepis* as also in *Picea bicolor*, there is a more or less pronounced tendency to an obliteration which is never fully developed. This is expressed in the somewhat remote position of the pits and

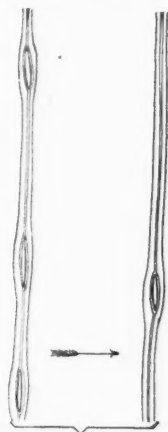


FIG. 11.—*Sequoia gigantea*. Radial section showing the bordered pits on the tangential walls of the spring wood. $\times 280$.

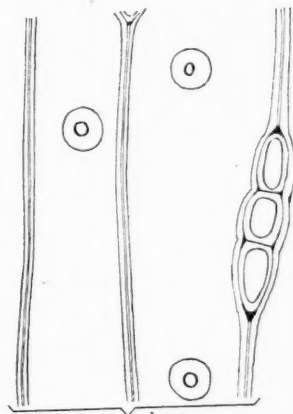


FIG. 12.—*Sequoia gigantea*. Radial section showing bordered pits on the tangential walls of the spring wood. $\times 280$.

their very small size, which renders them obscure and often difficult to discover. In this respect these species represent transitional forms.

As an exceptional feature, bordered pits may sometimes be found upon the tangential walls of the spring wood. This is especially noticeable at the ends of tracheids, and in rare cases it may apply to the entire extent of the wall. The most notable instance of this kind, because practically unique, is to be met with in *Sequoia gigantea* (Figs.

11, 12). Those spring tracheids which lie in direct contact with the summer wood of the previous year, often exhibit this feature with great prominence, but it may also extend radially through several successive tracheids. This is undoubtedly a primitive character, and in the one case cited it possesses some value for the purpose of specific differentiation, but in general terms, the occurrence of bordered pits in such positions is of so sporadic a nature as to give this feature no well defined value, either for taxonomic or phylogenetic purposes. It may, nevertheless, be stated with respect to the pits on the tangential walls of the tracheids in general, that in their distribution they distinctly conform to the law governing similar structures on the radial walls.

Reference to *Cordaites acadianum* shows that in the multiseriate pits of the hexagonal form, these structures always preserve the spiral arrangement characteristic of the structures from which they were derived (Fig. 4), and this conformity also extends to the direction of the spirals which generally ascend from left to right. The general law in this respect has already been formulated so fully by De Bary (9, p. 163), as to make it unnecessary at this time to enter upon its consideration more in detail, beyond a reference to one or two special features and some apparently exceptional cases. While the spiral arrangement is always typical in such genera as *Cordaites*, *Agathis*, *Araucaria*, etc., it is not obvious in those cases where the pits are strictly uniseriate and often remote from one another. Nor is it apparent at first sight in those cases of 2-seriate pits where, as in *Cupressoxylon dawsoni* from the Cretaceous, *Larix americana*, *Sequoia* and various species of *Pinus*, the pits are always paired off in such a way that the axis of each pair is at right angles to the axis of the cell (Fig. 7). Two explanations are here possible: (1) the spirals are in reality 2-seriate, and they are projected through the alternate members of the two rows of pits, or (2) the disposition of the pits represents an extreme phase in the flattening of the original spirals conformably to a higher type of development. This latter view, which seems the more reasonable, is in direct harmony with De Bary's law, while it receives additional support from the form and direction of the pit orifice.

The orifice of the pit is variable, at different times being round, when the pits are also round and more or less distant; oval or oblong, when the pits assume corresponding forms; or in the summer wood, lenticular or oblong. The transversely elliptical pits of *Pinus strobus* (Fig. 8), the orifice of which is also transversely oblong, as also the similar pits of *Pinus cubensis* (Fig. 7), afford substantial proof in confirmation of the probable correctness of this view. In the summer wood, the pit orifice commonly assumes a position which appears to offer a direct contradiction of this conclusion. In *Pinus strobus* (Fig. 9), the orifice is oblong and parallel with the tracheid axis. In *Pinus pungens*, as in many others of the same genus (Fig. 13), the narrow orifice is extended above and below into a diagonal slit of great length, forming a narrow angle with the tracheid axis. At first sight this would seem to imply that these features represent primitive

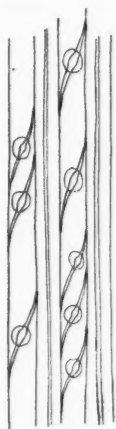


FIG. 13.—*Pinus pungens*. Bordered pits on the radial walls of the summer wood. $\times 280$.

spirals, the original direction of which has not been greatly if at all modified, but one or two considerations will assist us to a correct interpretation of this feature. In the first place it is to be observed that such positions and modifications of the orifice are invariably associated with the summer wood, or where they occur in the spring wood, it is the result of maceration and commonly occurs in fossil plants, or woods in process of decay, and they are always most conspicuous in those tracheids which have experienced the most profound modifications with respect to the growth in thickness of the secondary walls. It has already been shown in the case of *Taxus* and *Torreya*, that there is no necessary connection between the spiral bands and the spiral lines of striation—that, as a matter of fact, as particularly illustrated by *Torreya taxifolia*, the two are quite distinct from one another under ordinary conditions of development. But in cases where the wall experiences extreme growth in thickness, the obliteration of the original spiral structure is complete, and at the same time it is replaced by the normal striation of the wall which,

in such cases becomes most pronounced. Instances such as

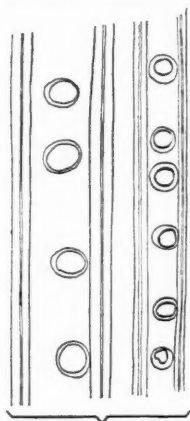


FIG. 14.—*Cupressus nootkatensis*. Radial section showing deformed bordered pits. $\times 280$.

feature in *Ephedra* and *Pinus sylvestris*, and he correctly interprets it as a form of arrested development. Alterations also arise as a feature of secondary growth in those cases in which the wall acquires unusual thickness. This is typically the case in *Pinus cubensis* where in plan (Fig. 15), the

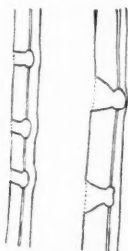


FIG. 16.—*Pinus cubensis*. Tangential section of bordered pits as in Fig. 15. $\times 280$.

orifice is extended vertically to a length often twice the diameter of the original pit. In tangential section, according to the particular direction of the plane of section (Fig. 16), the orifice is either of uniform width, or it enlarges constantly through the entire thickness of the later growth, from within outwards. That such unusual forms are features of extreme, secondary growth of the wall, and that they may be anticipated in all cases where such modifications of the walls occur, is a reasonable deduction from the observed facts.



FIG. 15.—*Pinus cubensis*. Radial section showing deformed bordered pits. $\times 280$.

TAXONOMIC AND PHYLOGENETIC.

For taxonomic purposes, the bordered pits possess a definite though often limited value. In the genus *Cordaitea*, as also in *Araucarioxylon*, *Araucaria* and *Agathis*, this is expressed in the hexagonal form together with their very compact, chiefly multiseriate arrangement throughout the entire extent of the tracheids, — characters which are of generic value and at once serve to separate these genera from all others. The contrasting differential feature is then to be found in the pits of the oval or round form, together with their 2-seriate or 1-seriate disposition with a more or less marked tendency to segregation. This is characteristic of the Ginkgoales and all the Coniferales, both fossil and recent.

As a different character of sub-generic value, the occurrence of bordered pits on the tangential walls of the summer wood of the first section of Pines — the soft pines — and their invariable absence from the same structural region in the second section — the hard pines, — is one which may be always relied upon.

For the purposes of specific differentiations, the pits on the tangential walls possess a distinctly inferior value which must be confirmed in most cases by the evidence of other factors. Their utility in this respect is made sufficiently clear in the various diagnoses and in the artificial key, without further discussion at this time.¹

In the genus *Cordaitea*, according to the provisional specific differentiations of fossil forms as at present generally employed, the number of rows of pits, or their segregation into definite groups, are characters of well defined, specific value, since they are among the few features which may be utilized with certainty for this purpose. Thus *C. acadianum* with its 2-5 rows; *C. materiarium* with 2-4 rarely 3-4 rows; *C. hamiltonense* with two rows and *C. newberryi* with two rows in groups of 6-13 pits, rest upon a basis which is not only easy of recognition, but which may be applied with full assurance, as has been done

¹ This paper will appear in the *Trans. Royal Society of Canada* for 1904.

on former occasions (38, p. 51 et seq.) In *Araucaria*, the three species investigated may be similarly differentiated from one another. The same rule is applicable to *Torreya taxifolia* which is thereby separable from the other species; likewise to *Cupressoxylon dawsoni*, *Tsuga canadensis*, *Larix americana*, and, among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis*. It is to be observed, however, that the constancy which characterizes this feature in *Cordaite*s and *Araucaria*, is wanting in the higher *Abietinæ*. In *Larix* there is such variation that very careful scrutiny is required, while in the genus *Pinus*, the number of exceptions to the typical character increases greatly, and is liable to cause some difficulty in the final determinations unless much care is exercised. *Pinus tæda* offers a conspicuous illustration of this fact, as may be seen by reference to the analytical key. It is therefore manifest that the value of the bordered pits for taxonomic purposes is most clearly defined in the lower types of the *Coniferales*, and that their value diminishes steadily, with an advance toward higher forms of organization and development. In all cases where exceptional forms introduce diagnostic difficulties, these may be overcome by the controlling effect of associated characters.

We are now in a position to examine the data at hand with a view to determining the bearing of the bordered pits upon questions of phylogeny.

Having reference to the origin of the bordered pit and the various modifications it presents in the course of development, it cannot be doubted that the hexagonal, multiserial pits of *Cordaite*s, *Araucarioxylon*, *Araucaria* and *Agathis* place those genera in a relatively inferior position, a view which gains a large measure of support from the well known and extensively multiserial disposition shown in *Heterangium grievii* (49, p. 341), but the facts so far discussed have not as yet thrown any special light upon the relative positions of the separate genera.

An examination of twelve species of *Cordaite*s shows that the bordered pits exhibit a much wider range of serial variation than any other genus covered by the present studies. If then we accept the general principle with respect to the development of the bordered pits as already illustrated, it cannot be doubted that

the 2-5-seriate pits stand much nearer to the primitive form of the tracheid than do the 1-seriate. From this point of view it is then evident that in *C. recentium*, the name of which is thereby seen to be fully justified, the 1-seriate pits place it at the upper end of a series which has its inferior termination in the 2-5-seriate *C. acadianum*, while between the two, intermediate forms appear as members of a series of nine variants, and it is possible to arrange these in such a manner as to exhibit the probable sequence in development as follows:—

Serial variations in the Bordered Pits of Cordaites.

	2-5 ser.	3-4 rarely 2.	2-4 chiefly 3.	3-4 chiefly 2.	2-3 rarely 4.	2-3 chiefly 2.	1-3 chiefly 2.	2-ser.	1-ser.
<i>C. acadianum</i>	x								
<i>ohioense</i>		x							
<i>ouangondianus</i>			x						
<i>materiarium</i>				x					
<i>clarkii</i>					x				
<i>annulatum</i>						x			
<i>brandlingii</i>							x		
<i>materioide</i>							x		
<i>illinoisense</i>							x		
<i>hamiltonense</i>								x	
<i>newberryi</i>								x	
<i>recentium</i>									x

The wide range of variations here shown, especially when compared with other genera, at once serves to suggest that *Cordaites* was in this respect somewhat of the nature of a transition group from which others were given off, or else that it epitomized the collective changes through which a number of genera must have passed. And inasmuch as this genus exhibits a more highly developed, multiseriate arrangement than any other within the general phylum, we must concede that it is, with respect to this character, the most primitive of all.

The genus *Araucaria* shows a much more restricted range of variations, there being only four variants pretty uniformly distributed among fourteen species, both recent and fossil. While the most highly developed members, four in number, are represented by 1-seriate pits, the most primitive form of 4-seri-

ate pits occurs in only one case — *A. robertianum*. It is therefore manifest that this genus is obviously of a more advanced type than Cordaites from which it undoubtedly originated. Agathis being represented by only one species, it is not possible to locate it more definitely than to say that the 1-3-seriate disposition of its pits would place it in a position equivalent to that occupied by *Araucaria cunninghami* and therefore about three-fourths way down the scale for that genus. This fact points with much force to the idea that of the two genera, Agathis is of relatively lower type.

The Ginkgoales and the Coniferales as a whole, exhibit an obviously higher type of development than the preceding group, in consequence of the more pronounced tendency to segregation of the pits which are now either elliptical or round, and never hexagonal. This distinction is so clearly defined and constant as to support the idea which gains force in other ways, that Cordaites, Araucaria and Agathis are clearly related members of a principal branch of the original stock, and that they therefore diverge considerably from the particular line of descent within which we find both the Ginkgoales and the Coniferales.

The observations so far made apply altogether to the pits on the radial walls. We may now pass to a consideration of their relation to the tangential walls, a factor which does not call for very extended discussion. This feature is found to apply to 71.7 % of all investigated species exclusive of fossils. It is wanting in three species of Araucaria, representing 2.58 %; in Torreya, 2 species or 1.72 %, and in the entire second section of Pinus to the extent of 28 species or 24.1 %. But the occurrence of pits on the tangential walls, in common with those on the radial walls, is a well known feature of the Sigillarias (49, p. 198), where their primitive character is well established, and we can hardly doubt that their ultimate elimination in the higher pines is the expression of a final phase in development, consistent with the position usually assigned those plants. The absence of pits from the tangential walls of certain Araucarias and Torreya, is to be interpreted as one of those sporadic tendencies toward a higher type of development which never become permanent in the same line, but which are to be met with as one of the invariable features of evolution.

Ginkgo, being the unique representative of an ancient line, cannot very well be brought into the present discussion very much in detail. On other grounds it is known to be a primitive form representing a group distinctly inferior to the Coniferales, and this view is supported by the disposition of the pits in two series, a character which, if taken alone, would give the genus rank with *Torreya taxifolia* among the Taxaceæ, but when regarded collectively, would place the genus distinctly below the Coniferales as a whole. This evidence, then, indicates that the Ginkgoales must have arisen as a side line at some point inferior to the Coniferales, but superior to the Cordaitales.

In the Taxaceæ the bordered pits do not in themselves afford very conclusive evidence as to the relative position of the family. Among the eight investigated species, representative of three genera, only three, and chiefly two variants occur. Taken alone, the disposition of the pits would lead to no final conclusion, but other factors permit of placing this family in the inferior position usually assigned to it. Within the genus three variants are found—the 1-2 rows of *T. taxifolia*, the one row or pairs of *T. californica* and the strictly 1-seriate form of *T. nucifera*. In *Taxus* only two variants appear—the one row or pairs of *T. floridana* and the 1-seriate disposition as found in the remaining three species. The one representative of *Podocarpus* shows but one variant, and that is 1-seriate. From this it is obvious that the generic sequence must be in the order given, and that the sequence of species must be approximately as given in the table of anatomical data to follow.¹

The remaining genera of the Coniferales present so few deviations from a typical form, that they cannot be differentiated fully on the basis of the bordered pits. This character nevertheless has a definite value in association with others, as in the genus *Sequoia* or some of the hard pines, *Larix americana*, etc. The general sequence of genera may be recognized by the bordered pits only in so far as these structures serve to confirm and emphasize the conclusions reached in other ways, and this will become apparent from an inspection of the table of anatom-

¹ This table will appear in the last number of this series.

ical data. It will nevertheless serve a useful purpose at the present moment, to ascertain the general sequence based upon the percentage distribution of the principal variants as follows.

Comparison of the principal variations in the serial arrangement of bordered pits, by percentages.

	Total var.	2-5	2-4	2-3	1-3	2	1-2	1+ pairs.	1
<i>Cordaites</i> . .	9	8.3	25.0	16.6	25.0	16.6			8.3
<i>Agathis</i> . .	1		6.6	20.0			40.0		33.3
<i>Araucaria</i> . .	4		6.6	20.0			40.0		33.3
<i>Ginkgo</i> . .	1						100.0		
<i>Sequoia</i> . .	1						100.0		
<i>Larix</i> . .	3						33.3	33.3	33.3
<i>Taxodium</i> . .	2						25.0		75.0
<i>Libocedrus</i> . .	1							100.0	
<i>Thuja</i> . .	1							100.0	
<i>Pseudotsuga</i> . .	2							50.0	50.0
<i>Pinus</i> . .	3						17.1	41.5	41.4
<i>Abies</i> . .	3						13.6	27.3	59.1
<i>Taxus</i> . .	2							25.0	75.0
<i>Tsuga</i> . .	3						16.7	16.7	66.6
<i>Picea</i> . .	2							10.0	90.0
<i>Podocarpus</i> . .	1								100.0
<i>Thujopsis</i> . .	1								100.0
<i>Cryptomeria</i> . .	1								100.0

With respect to specific differentiations, it has already appeared that the bordered pits may be employed with success in *Taxus* and *Torreya*. In *Cupressus* this rule also applies to *C. pisifera*, and *C. macrocarpa*, both of which are distinguished by having their pits in one row or pairs, while the remaining seven species have strictly uniseriate pits. An instructive example is afforded by *Cupressoxylon dawsoni*. In this species, which is of early Tertiary age (Lignite Tertiary), the pits are typically 2-seriate, being disposed in a very compact manner similar to that found in existing *Sequoias*. But in a series of eleven specimens, it is clearly seen that two variants are represented—the second being a 1-seriate form. These variations are also found, as in the other Coniferales, to be directly related to variations in the size and rate of growth of the tracheid. It cannot be doubted then, that *C. dawsoni* is a more primitive representative

than any species now existing, and that it is substantially the ancestral form of the genus, so far as we know.

In *Larix* the four investigated species may be differentiated pretty fully, and this rule applies with particular force to *L. americana*, and *L. occidentalis*, both of which are distinguished by a 2-seriate form. Among the pines, *P. lambertiana*, *P. clausa*, *P. sabiniana*, *P. tæda*, *P. palustris*, and *P. cubensis* are readily differentiated from the others by the 2-seriate pits. In all other cases than those specifically indicated, the bordered pits afford an inadequate basis for specific differentiation.

It is now apparent that segregated, round or oval pits in one row must be taken as representing the highest type of development in the Coniferales, and any deviation from this must be taken to indicate the survival of more primitive conditions, pointing to derivation from a type like that of *Araucaria* or *Cordaites*. From this point of view, the occurrence of pits in 1-2 rows in *Larix americana*, *Torreya taxifolia*, *Sequoia*, *Tanga canadensis* and various species of *Pinus*, indicates the survival of ancestral characters which are partial to the extent of 7.2 %, and complete to the extent of 10.8 %. That such deviations from the usual type of structure are either survivals or reversions which serve to indicate a common origin, cannot be doubted, more especially as they do not occur at a fixed point near the original type, but they arise sporadically in widely separated genera. The tendency of such evidence then, is to show a common ancestry for the various genera of the Taxaceæ and Coniferaæ, a view which is greatly strengthened by the testimony afforded by the spiral tracheids of *Larix americana*, *Pseudotsuga* and *Pinus tæda*. The provisional conclusions which we now reach are, that there were probably four main lines of descent from the original stock represented by *Cordaites*:

- 1 *Araucaria* and *Agathis*.
- 2 *Ginkgoales*.
- 3 Taxaceæ.
- 4 Coniferaæ.

(To be continued.)

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF
THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD
COLLEGE. E. L. MARK, DIRECTOR.—No. 151.

THE SENSE OF HEARING IN THE GOLDFISH
CARASSIUS AURATUS L.

HENRY B. BIGELOW.

I. INTRODUCTION.

TO THE older investigators, such as Hunter (:82) Müller ('48), and Owen ('66), the presence of internal ears in fishes was sufficient evidence that these animals had a sense of hearing. Kreidl ('95), however, was the first to seek experimental evidence on this point. He tested normal goldfishes, and others from which he had removed the semicircular canals with the attached portions of the ears. Since both classes of fishes reacted similarly to sounds, he concluded that the skin, not the ear, is stimulated by sound, and that, therefore, it can be said that goldfishes do not hear. This conclusion has since gained considerable recognition, and has been accepted by Mulerdt (:02) in his recent book *The Goldfish*. Kreidl ('96) also made observations on the trout in the fish basins of the Benedictine Monastery at Krems, Austria, and gathered ample evidence to prove that the belief that the fish assembled for food at the ringing of a bell to be unfounded. These observations confirmed him in the opinion that fishes do not hear, a conclusion further supported by the subsequent observations of Lee ('98) on other species, particularly the dogfish.

In spite of this important evidence, Lang (:03) concludes a popular discussion of the question "Do aquatic animals hear?" with the statement that fishes and other like forms should be tested more extensively before a decisive answer can be given. Tullberg (:03), whose experiments led him to conclude that the fish ear receives stimuli from currents in the surrounding water,

admits the possibility that the ear may also be in some degree an organ of hearing. The fact that certain fishes do respond to what are beyond question sound vibrations in water was demonstrated independently by Zenneck (:03) for three fresh-water species, *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus*, and by Parker (:03^a, :03^b) for a salt-water species, *Fundulus heteroclitus*. Parker further showed that this response was dependent on the presence of a functional internal ear, and that, therefore, this species could be said to hear. But he could not get any response to sound from the smooth dogfish, and so was led to conclude that different fishes might differ widely in this respect, some possessing, some lacking, a true sense of hearing. Since none of the recent investigators who favor the view that fishes hear, have tested the species which, in Kreidl's hands, yielded negative results, it seemed desirable, in the light of recent work, to examine the goldfish again; and this I have undertaken to do. This problem was suggested to me by Professor G. H. Parker, and I am indebted to him for help, suggestions, and criticism throughout the series of experiments.

II. METHODS.

In determining whether or not a fish has a sense of hearing it must be borne in mind that the responses to sound may be very slight and easily confused with responses to other stimuli; and, further, that, although the absence of response does not necessarily mean absence of hearing, the consistent occurrence of a response is fair evidence of the presence of this sense. To test normal goldfishes satisfactorily, it was necessary to isolate them from all other disturbances and to apply the sounding instrument as directly as possible to the water, but without causing any gross mechanical vibration. The apparatus which I used was an aquarium, some 30 cm. wide, 35 cm. long, and 15 cm. deep. The two sides were of glass, and the ends and bottom of clear white pine. The aquarium was placed on a wooden table which stood with its feet on many thicknesses of soft paper, thus isolating it from vibrations which might otherwise reach it through the floor. The bottom of the aquarium was covered on

the inside with a thick layer of cotton wool, which, in turn, was held in place by a sheet of thin cotton cloth to form a deadened floor. On trial, I found that the light entering through the glass sides of the aquarium was a source of disturbance to the fishes. Hence I later made these sides opaque by a covering of dark paper. My method of producing sound was by an electric tuning fork, which was run by a small storage battery and had a pitch of 100 vibrations per second. This was set up on another table, very close to the first one, but not in contact with it. The foot of this table also stood on many thicknesses of soft paper. The fork itself rested on a deadened support, and was so arranged that after it had been set in vibration, it could readily be moved till its base came in contact with the wooden end of the aquarium. This could easily be accomplished without observable jar to the water in the aquarium, and certainly in itself had no effect on the fishes. For when I made the fork, not in vibration, touch the aquarium in the usual way, the fishes gave no reaction, although to the vibrating fork they were very responsive; I tried this many times.

With this apparatus, I tested three classes of goldfishes; (1) normal ones; (2) fishes the greater part of whose integument had been made insensitive by cutting the fifth and seventh nerves, the lateral line nerves, and the spinal cord close to the medulla; and (3) fishes in which the eighth nerves had been cut.

III. NORMAL FISHES.

Goldfishes appear to be much more irregular in their responses to sound than some other fishes. When one is first placed in the aquarium, it swims about vigorously, darting from side to side in a very restless fashion. This extreme excitability lasts for a considerable time, often an hour; but finally the fish becomes more quiet, sinks to the bottom, and remains nearly motionless except for an almost incessant movement of the pectoral fins. In a few cases, the fishes lay motionless with these fins folded closely to their sides. If now the tuning fork was set in vibration, and brought into contact with the wooden

end of the aquarium, the fishes almost always responded by one of a number of reactions. The most important of these were: a rapid vibration of the tail without locomotion; sudden jerks of the tail from side to side, often so vigorous as to cause a swift dart forward; normal locomotion, forward, backward, or to one side; or in those fishes which lay at rest with the pectoral fins folded, a vigorous spreading of the pectorals. It was evident that individual goldfishes differed from one another in their reactions much more than the individuals of *Fundulus* as recorded by Parker (:03^a, p. 51). When a fish was tested with the vibrating fork, it might respond by any one of these reactions, but every fish had one distinct reaction characteristic of it, which the application of the fork rarely failed to elicit. Thus, the more active fishes usually responded by vigorous locomotion, the more quiescent ones, by tail or fin movements. Although fishes on which no operation had been performed, usually responded to the sound, one, an albino, and a very sluggish individual, gave no response. The fact that this one died soon after my observations on it were made, is perhaps an explanation of its unusual condition. As an example of the characters of the responses, the following record of ten tests from my laboratory note-book may serve. This record relates to a fish which was subsequently operated upon by cutting the eighth nerves.

1. Tail-jerks, followed by forward swimming.
2. Tail-jerks, then forward swimming after an interval of half a second.
3. Sudden tail- and trunk-jerks, followed by forward swimming.
4. Tail-jerks, but without locomotion.
5. Tail-vibration, but without locomotion.
6. Strong tail-vibration followed by a turn to one side.
7. Tail- and trunk-jerks, followed by forward swimming.
8. Tail-vibration, followed by a sudden turn to one side.
9. Tail- and trunk-jerks, followed by a turn to one side.
10. Tail-jerks, and sudden jump forward.

In all, I made 193 tests on 18 normal fishes, and observed 150 responses, about 78% of the whole. Of the 43 failures, to

respond, 12 were in the case of the albino fish above mentioned, and many of the remaining 31 were probably due to faulty observations caused by the extreme activity of the fishes. In this respect, there is a great difference between different individuals, some being in such continual movement that it is difficult to test them, while others are more generally quiet.

IV. FISHES WITH INSENSITIVE SKINS.

The second class of fishes tested were those in which the greater part of the skin had been rendered insensitive by cutting the spinal cord just posterior to the pectoral fins, as well as both lateral branches of the tenth, and the fifth and seventh nerves on both sides of the body. The fifth and seventh nerves were cut at a point just above the dorsal end of the opercular opening, where they come close to the skin. The fishes were etherized before the operation, and usually recovered and lived many weeks. The individuals selected for this operation were those which showed good pectoral-fin reactions when tested with the tuning fork. Such fishes after recovery lay on their sides on the cloth bottom of the aquarium, and were perfectly quiet unless stimulated. That their skins were practically insensitive was shown by the fact that they were quite indifferent to touch with a bristle or the like.

In 65 tests on 6 such fishes, I observed 52 responses (80%) to the vibrating fork, a condition essentially the same as that of normal fishes. These experiments demonstrate then, that with an almost insensitive skin, a goldfish will respond to sound as a normal fish does.

V. FISHES WITH INSENSITIVE EARS.

The third class of fishes tested were those in which the eighth nerves had been cut on both sides. In preparing for this operation a number of fishes were tested and only such as showed a clear reaction to sound were operated on. They were etherized, and their eighth nerves were cut by piercing the skull in an appropriate position and cutting downward with a small chisel-

like knife. The chief danger in this operation is in cutting too deep, in which case excessive bleeding may follow. When this was avoided, the fishes usually recovered, and the success of the operation could be judged by their subsequent movements. When they first recovered from the ether they seemed to have lost all power of equilibration, swimming now one side up, and now the other, or resting with their long axes vertical. After about a day, however, they usually acquired and kept their normal position, at least while resting or swimming slowly; and this ability increases, until after two or three weeks they were, in all their ordinary movements, indistinguishable from normal fishes. If, however, such a fish be placed in a large body of open water and made to swim rapidly, it soon loses all power of orientation and darts about, turning over and over until exhausted. This condition, so far as I know, is permanent, for in the case of one fish which lived for over three months after the operation these reactions showed no tendency to disappear, but persisted till death. The partial recovery of equilibrium noticeable soon after the operation is probably due to a successful attempt on the part of the fish to retain its normal position through sight.

Earless fishes are usually more quiet than normal ones, and hence they can very easily be tested. In all, I made 73 tests on 7 fishes, and in no instance did I get an undoubted response to sound. This is in strong contrast with the reactions of the same fishes before their eighth nerves had been cut, and points beyond question to the ear as an organ of hearing.

I supplemented the foregoing experiments by another series in which two normal fishes that I found to respond well to sound, were etherized, and the eighth nerve of each cut on the right side. After an interval of twenty-four hours, they were both tested again, and found to respond about as well as they did before the operation. In 20 tests on the two, there were 19 responses. They were then etherized again, and the eighth nerves of the left sides were cut. After recovery, they were tested once more, and, although the experiments were conducted with the greatest possible care, not a single response was observed in 20 trials. This experiment shows that the

operation of cutting the eighth nerve, severe as it is, is not sufficiently so to account for even a small part of the reduction in the number of responses which follows the elimination of both ears as sense organs.

In another instance, a fish which before any operation responded vigorously to sound by movements of the pectoral fins, was prepared by cutting two holes in the top of the skull, through which the eighth nerves could conveniently be reached, and the following parts were severed: the spinal cord, the lateral line branches of the tenth nerves, and the superficial portions of the fifth and seventh nerves of both sides. After recovery, the fish gave ten vigorous pectoral fin responses to as many trials with the sounding apparatus. The eighth nerves were then cut, and in twelve tests only one response, and that of a doubtful character, was observed. It, therefore, seems incredible that nervous shock can account for the almost complete loss of response to sound, after cutting the eighth nerves, and I am firmly convinced from the foregoing experiments, that the ear in the goldfish is an organ of hearing, and that it is the loss of this which is accountable for the difference of reaction between fishes in which the ears were intact, and those in which the eighth nerves had been cut.

VI. DISCUSSION OF RESULTS.

The results of my experiments differ so essentially from those obtained by Kreidl ('95) that a further discussion of these differences is necessary. So far as reactions to sounds were concerned, Kreidl was unable to distinguish between normal goldfishes and individuals from which the semicircular canals with the attached parts of the ears had been removed. In my experiments, however, while normal fishes responded to sound in about 78% of the trials, those in which the eighth nerves had been cut, scarcely responded at all. The difference between these two sets of results was so great that I determined to repeat, with as much precision of detail as possible, Kreidl's experiments.

I tested several goldfishes, and, having found that they

responded well to the tuning fork, I operated on them in the following way. After etherizing the animals, I cut off the top of the skull, exposing the brain, and the vertical semicircular canals. I then seized the canals with forceps and drew them out bodily with the attached sacs and their otoliths, as Kreidl had done. I operated thus on four fishes, three of which recovered. After recovery, I tested them again with the tuning fork, and found that one responded to the sound about as well as before the operation, and that the two others responded somewhat less regularly than before, though in a still perfectly definite and unmistakable manner. Thus, since these fishes responded like normal individuals, my results confirmed in all essential respects those of Kreidl, and I came to the conclusion that there must be some fundamental difference between Kreidl's methods for the elimination of the ear, and mine. The method I generally used, cutting the eighth nerves, seemed to me a perfectly secure means of excluding the action of the ear. On the other hand, the withdrawal of the semicircular canals with the attached parts of the ear, as practiced by Kreidl, might well leave behind and intact parts of that organ, and thus be inefficient as a method for completely excluding the ear. To settle this matter, I made careful dissections of the ears of goldfishes. The ear of the goldfish is in all essential respects similar to that of *Cyprinus*, as described and figured by Retzius ('81, p. 78). The semicircular canals are of large size; the two vertical canals lie free in the brain cavity, while the horizontal canal is partially imbedded in the skull. The sac into which these canals open, the utriculus, is of medium size, and contains a large lenticular otolith. The utriculus, with its otolith lies free in the brain cavity and is the structure which is removed in connection with the semicircular canals in fishes which are operated on by Kreidl's method. But ventral to these parts, and largely imbedded in bone is another portion of the internal ear, which probably represents the combined sacculus and lagena. This is not removed, nor even seriously disturbed by the Kreidl operation. This deeper sac extends posteriorly and ventrally until that of the right ear nearly meets that of the left in the base of the cranium. Each sac contains two otoliths, one long and

rod like, lying for the most part in the saccular portion, the other lenticular in outline, and lodged in the lagena proper. The wall of this sac is supplied with branches from the eighth nerve and is so surrounded by bone that all attempts to remove it by pulling out the semicircular canals were complete failures. In the four fishes on which I operated by Kreidl's method, subsequent dissection showed these structures intact. Thus, his operation leaves uninjured a large part of the internal ear, in fact, just that part which, from comparison with the ears of higher vertebrates, would be expected to be concerned with hearing. I believe, therefore, that Kreidl's method of operating is defective, and the reason that the fishes upon which he had operated responded to sounds much as normal ones did, was not because in both cases the skin was stimulated, as he believed, but because his so-called "earless" fishes still retained intact a part of the ear which, as I have already shown, acts as an organ of hearing. That it is such an organ follows from the fact that when its nerve connections are cut, the responses to sound cease.

VII. SUMMARY.

1. Normal goldfishes usually respond in a definite manner to sound-vibrations in water.
2. Goldfishes in which most of the skin has been rendered insensitive by cutting the nerves, and specimens from which the ears, except the saccular portion, have been removed still respond in an essentially normal way to sound vibrations in water.
3. Goldfishes in which the eighth nerves have been cut on both sides, thus eliminating the sacculi and lagenæ as well as the rest of the ear, seldom or never respond to sound vibrations in water.
4. Goldfishes possess the sense of hearing, and the portion of the ear concerned with this sense is the sac which probably represents the sacculus and the lagena of higher vertebrates.

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CERTAIN UNDETERMINED FACTORS IN HEREDITY AND ENVIRONMENT.

GEORGE J. PEIRCE.

IN a paper read before the Botanical Section at the Pittsburg meeting of the American Association for the Advancement of Science ¹ I suggested that certain factors of the environment were constantly ignored in such discussions of heredity as I had seen or heard. This paper constitutes substantially the last section of my book.² Since certain letters which I have recently received, make me feel that in this section I have expressed myself so concisely that my full meaning is not altogether clear, I take this opportunity to give somewhat ampler treatment to the subject.

The word *environment* is used ignorantly by everyone, for no one has ever succeeded in making a complete analysis of what is meant by this collective term. Furthermore, although we speak of an organism as reacting to its environment, it does not react to its environment as a whole but to each of one of the separate influences which are the factors of its environment. It is, therefore, very important to know what these factors are, and what are their effects. We know that if two of these influences are opposite and equal, there will be no visible reaction, although the organism will be affected by both. There may be internal results of these influences, results which, however, may not be perceptible. If one of these opposite influences be lessened or eliminated, the effect of the other becomes perceptible. We judge, then, the influence of the various factors which we are now able to distinguish from one another as constituting the environment, only by their perceptible effects. It is conceivable that some effects are so long deferred that they are coincident or at least contemporaneous with the effects of other and more recent stimuli. For this reason these long deferred effects may

¹ Abstract in *Science*, XVI. p. 137, 1902.

² Peirce, G. J. *Text book of Plant Physiology*, 279-83, New York, 1903.

easily be overlooked, or they may be perceived only incompletely and with difficulty, or they may be attributed to wrong causes. It is also conceivable that certain influences produce effects not because they are powerful, taking into account only short times of operation, but because they are prolonged.

This leads us to essay an analysis of environment. The environment of an organism is all, everything, that constitutes the world and the universe outside of itself. One may say that this definition is too comprehensive, that only *immediate* environment is meant when the word environment is generally used. Who can say that organisms and things are affected *only* by their immediate environment? In fact we know that the contrary is true in certain particulars. We know, for instance, that we are daily affected by the sun — a remote body — quite as much as by any part of our immediate environment. But we do not know all the radiations and other influences from all the heavenly bodies in the universe, the effects of these upon our earth as a planet, and what is upon it; and yet these radiations still unknown and unguessed, together with other unknown and unguessed factors of environment, may operate as regularly and as powerfully as any of the known and recognized factors.

Among the recognized factors of the environment are some, the effects of which are very imperfectly known, if they may be said to be known at all. These will be seen in their relations to other factors if an analysis, however imperfect, of the environment be given. Thus

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|---|---|---|
| Environment —
all that consti-
tutes the uni-
verse. | { | <ol style="list-style-type: none"> 1. <i>The earth</i> — soil, rocks, waters, atmosphere; the components, conditions, contours, etc., of these. 2. <i>All other planets</i> — whatever conditions prevail upon them; their relative positions to the earth and to each other. 3. <i>The forces</i> emanating from and operating upon these — heat, light, electricity, mechanical forces (gravity, wind, waves, rain, etc.). 4. <i>All living things</i> — their parts, products, and habits. |
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If we go through the list of factors suggested by this scheme,

we shall see that, in spite of their diversity and oppositeness, we may bring them into an orderly classification. We may arrange them under these four headings — 1, unchanging, 2, variable, 3, occasional, 4, periodic. Among unchanging factors the following may be mentioned,¹ *viz.* the atmosphere, water, the force of gravity, the earth as a whole. Though these are not all of the unchanging influences I shall discuss only these four.

The earth's atmosphere, consisting of nitrogen (80%) and oxygen (20%), with only a small fraction of 1% of carbon-dioxide and other gaseous matters, possesses unchanging physical properties and exerts a pressure which varies only very slightly, taking only short intervals of time for the comparison, and varies not at all, taking long intervals of time. For example, the barometric pressures in any given locality are the same in this century as in the last, and though we may have "low" and "high" barometers at different times, these variations are very slight. The buoyancy, diversity, color, transparency, permeability, etc., of the earth's atmosphere are the same to-day as a "million" years ago, as far as we know, and though these qualities and the pressure of the atmosphere may change and may have changed during the lapse of the millions of years during which the earth is likely to exist and has existed as a planet, they are unchanging so far as millions of generations of living organisms, and so far as millions of series of lifeless things, are concerned.

The composition of the earth's atmosphere has changed but little, if at all. The proportion of carbon-dioxide may have been greater in an earlier time, but for uncountable ages the proportions have been what they are now. Let us suppose, however, that the proportions of nitrogen, oxygen, and carbon-dioxide have changed somewhat, taking the whole atmosphere into account, not a small part of it merely. If only the proportions were different, there would still have been nitrogen, oxygen, and carbon-dioxide in the air, and these gases themselves are unchanging. We cannot imagine some oxygen being any different from all oxygen; if we have carbon dioxide we have necessarily carbon-dioxide of the same composition and properties since the world began. The same of the inert gas nitrogen.

¹ See p. 280 of my "Text Book."

When experiments are instituted for the purpose of eliminating these substances, they fail, for it is out of the question to remove all nitrogen, oxygen, and carbon-dioxide even if all N, O, and Co_2 can be excluded at the beginning of an experiment, for N and O will be contained in the organism and Co_2 will be formed by it. Nevertheless, the living organism which is dependent upon oxygen for respiration, upon nitrogen to dilute the otherwise too destructive oxygen, and upon carbon-dioxide from which to manufacture food, will succumb in any experiment of more than brief duration in which the proportions of these gases are greatly different from those in normal air. In other words the physical properties of the atmosphere, its components, their composition and proportions, being and having for ages been what they are, living organisms represent reactions to these qualities and will not bear sudden change, whatever might be or may have been the result of gradual change, if there has been any.

Water is composed of hydrogen and oxygen in the proportions of two to one. It always has had the same chemical composition, structure, and properties, the same physical qualities. It is an indispensable constituent of living organisms and of many lifeless things. It is a weak acid and the most universal solvent known. Molecules and atoms of dissolved substances move about in it with considerable freedom, and where two volumes of water are separated from one another only by permeable or semi-permeable membranes, there is molecular or atomic movement both of water and of dissolved substance from the one volume to the other through the membrane. Water is then a medium in which ampler molecular and atomic movements are possible at ordinary temperatures, etc., than in many other substances. But the movement of the molecules and atoms of the solutes are independent of, though taking place among, the water molecules. The water remains the same, physically and chemically, whatever substances may be dissolved in it. The temperature of a solution of small volume may be different while solution is taking place, but ultimately the temperature of the solution, or of water holding nothing in solution, will be approximately that of its surroundings, other things being equal. The specific gravity of the solution will differ from that

of pure water, but the specific gravity of the water itself and of the solute itself are the same as they have always been, the specific gravity of the solution depending only upon these two.

With its physical and chemical properties unchanged, as an essential constituent of all living organisms and the medium in which necessarily the food materials and foods enter and move about and are chemically changed in the cell, water has exerted upon living things an influence as powerful and as persistent as have been its relations to the physical and chemical conditions and processes of lifeless substances since the beginning. Water can be eliminated neither outright nor by substitution from experiments with living organisms nor, for that matter, can it be eliminated from the majority of experiments with lifeless substances. It is a substance of universal occurrence, of uniform properties, of uniform action. It is truly one of the unchanging factors of the environment, to which living organisms necessarily react, for their composition, structure, nutrition, and activities depend upon it.

We come now to consider the effect of gravitation. The force of gravity acts upon every particle of ponderable matter on the earth as a direct pull toward the center of the earth. This pull is equal, at the surface of the earth, to 32.2 foot seconds², *i. e.* a body at the surface of the earth would fall in a vacuum at a rate increasing 32.2 feet a second per second. The force of gravity, operating upon every particle of ponderable matter, constantly exerts upon it this uniform force. The force increases or decreases inversely as the squares of the distances. But, as Newton showed, the force of gravity is not merely the attraction between the earth as a whole and other ponderable matters, but every portion of matter attracts every other portion with a force proportional to the product of their masses divided by the square of their distances apart.¹ The sum of the attractions toward the center of the earth equals the amount previously mentioned, 32.2 foot seconds², and this sum we may for the moment speak of as gravity without necessarily taking its components into account.

¹Watson, W. *A Textbook of Physics*, p. 121. New York, 1900.

The attraction of gravity upon all ponderable matters is, however, opposed by the media in which they are. This is implied by the statement of the value of gravity at the earth's surface, for this statement specifies *in vacuo*. Every ponderable body is bouyed up (or supported) by a force equal to the weight of the fluid it displaces. This law of Archimedes concerns us as it applies to the air and to both fresh and salt water. Besides, this we have the solidity and comparative impenetrability of the earth itself to reckon with, for the soil is capable of mechanically supporting much more than the weight of the parts of plants and animals resting upon or within it. Gravity is then opposed, partly or wholly, according to the medium in which the attracted object is.

The opposition to gravity varies from .0013 gr. per cc. in air at 0° C., and at ordinary atmospheric pressure, through 1.00 gr. per cc. in pure water and 1.20 gr. in sea water, to much more than the weight per cc. of any of the substances with which we ordinarily have to deal. Thus if we have a plant or animal or any other portion of matter weighing x grams in air, this matter would have a weight in pure water equal to x minus 1 gram for every cc. of volume. In sea water this would be $x - 1.2 y$, in which y represents the number of cc. in the portion of matter. To take a concrete instance, suppose we have a block of wood, occupying a space of 9 cc. and weighing 10 gr. in air. This would weigh in water $10 - 1 \times 9 = 1$ gr.; in sea water this would be $10 - 1.2 \times 9 = 0.8$ gr. or, in other words, the block would float. In the same way the block would be completely supported, gravity would be completely offset, if the block were on or in the soil. But as the soil, the water, and the air do not come into direct contact with and are therefore not displaced by each individual part and particle of a portion of matter, there must be enough mechanical strength within the portion of matter to resist the force of gravity or the body would fall to pieces. We see then that though a body as a whole may be bouyed up by a considerable force which resists gravity, the component particles of the body are not necessarily so bouyed up but are subjected to the full attraction of gravity. Although the bouyancy of the medium

in which a plant lives makes a very great difference in the mechanical strength of the plant as a whole,¹ there is no discoverable difference in the structure and other properties of the protoplasm. This fact is what the foregoing discussion has lead us to expect; for upon the component particles of protoplasm the force of gravity operates unopposed by the bouyancy of air or water, except such water as is in the cell-sap; and as the force of gravity is continuous and uniform in operation, the living protoplasm is subjected to a continuous and uniform influence. Does it not react accordingly?

Again, the force of gravity, regarded both as the attraction of the earth as a whole as well as the attraction of each particle of matter for every other, has never been eliminated from any experiment. If it had been, can we imagine what would have happened? The force of gravity acts only in one direction. The slow revolution of a plant upon a horizontal axis by means of a clinostat, so that all its parts will be successively turned in this direction, and the opposition of centrifugal or other force to the force of gravity, yield interesting results in experiments in which these methods are employed, but they throw little or no light on the influence of gravity upon the component parts of the living structure. Until gravity is eliminated, not merely opposed, we cannot even guess what its influence is; but rather than ignore it, we may guess that its influence as a formative agent is as great as we now know its directive influence to be. And as we know that its directive influence is always the same, that plants of a kind under like conditions respond in approximately like ways, like times, and with like force to the action of gravity, sending their roots downward into the soil and their stems upward into the air, we must infer that in the formation of new protoplasm the component parts of this structure are affected always in the same way and that they respond to the constant and uniform force in constant and uniform ways.

It remains to add a word as to the earth as a whole as one of the continuous and uniform factors of the environment of living

¹ Peirce, G. J. A comparison of land and water plants. *Pop. Sci. Monthly*, LXIII, p. 239, 1903.

organisms. The earth is a spheroid whirling in space at a rate decreasing with inconceivable slowness. Its position with relation to other bodies of the solar and other planetary systems changes also with inconceivable slowness. It possesses a degree and a distribution of heat throughout its mass which changes also with wonderful slowness. The earth possesses size, structure, composition, compactness, and other physical and chemical properties which change so slowly that in the lapse of ages differences can scarcely be detected, and millions of generations come and go under exactly like influences.

Passing now from these unchanging factors to the living organism itself, we must see that every particle of protoplasm is affected by the components and by the properties of the atmosphere, by the physical and chemical qualities of water, by the force of gravity, and by the earth as a whole. Every particle of protoplasm since it came into existence as such, every molecule of every compound in it, and every atom in the molecule, has existed from its beginning on this earth under these conditions and subject to these influences. None of these influences has ever been eliminated by experiment, nor has experiment ever resulted in accomplishing any fundamental change in a living organism or series of living organisms. Man as an experimenter cannot control these influences but is controlled by them. Is he not controlled by them in every other relation in life? Is man any more controlled by these unchanging influences than any other living or lifeless thing?

In the living substance of sperm and egg the component parts, particles, molecules, and atoms, have been subjected to these unchanging forces, not only since coming together as the living structure, but before; and after sperm and egg fuse the same is true; and in the growth of the fertilized egg every particle of new material is formed, placed, and kept in place under these influences. From the beginning to the end of its career every individual plant and animal is subjected to these continuous and uniform influences. But so also is every other thing. And as we find all common salt crystals behaving alike and being fundamentally alike at the same time that they are unlike the crystals of all other substances subjected to these

same influences, so we find the plants or animals of a kind behaving and being in the main alike at the same time that they are unlike the plants and animals of all other kinds, although they are subjected to the same influences. In the diversity of composition and adjustment to these forces we have a physical reason for the diversity of behavior of different animals, plants, and lifeless things. They are all influenced by these forces; what they are represents their reactions to these and to other forces. The fundamental likeness of parent and offspring represents the continuity of substance and of influence; the superficial differences represent the different influences to which they have been subjected and to which they have reacted. Not all common salt crystals are of exactly the same size. Not all the puppies of a litter are exactly alike. But the salt crystals are fundamentally alike, and so are the puppies. With their vastly greater complexity — considered merely chemically for the moment — one should expect puppies to vary more than salt crystals. But neither salt crystals nor puppies vary so far as not to be salt crystals or puppies; the continuous influences conserve their fundamental characters.

In this discussion two things have been assumed — the continuity of substance from parent to offspring, and the irritability the power of reaction, of this substance to the various factors of its environment. These two facts are essential to heredity. My contention is merely that in the continuous, unchanging factors of the environment we have forces, influences, stimuli, under the operation of which the living substance came into existence, under which it continues to exist, and to which it continuously and unchangingly reacts. These influences are factors in the environment, but at the same time, like irritability, they are factors in heredity. The clearer our conception and the fuller our knowledge of the irritability and the power of reaction of living organisms to external stimuli, the smaller the mass of unexplained though not unexplainable phenomena for which we shall make heredity accountable.



ON THE DENTITION OF RHYNCHODUS AND OTHER FOSSIL FISHES.

C. R. EASTMAN.

AMONGST Palæozoic chimæroids the complete dentition is known in at least two species of *Ptyctodus*, two of *Rhynchodus* and one of *Palæomylus*. These genera are all included in the family *Ptyctodontidæ* of the Devonian, and present for comparison with recent chimæroids a single dental plate on each side in the upper jaw, with a corresponding pair biting against the outer side of these (as shown by marks of contact) in the lower jaw. The question therefore arises whether the unique dental plate on each side in the upper jaw of *ptyctodonts* is homologous with the so-called "premaxillary" of *Chimæra*, *Callorhynchus*, *Rhinochimæra*, etc., or with the so-called "palatine plate" of the latter, or with both premaxillary and palatine taken together.

This question appears to be answered conclusively in the case of *Ptyctodus*, from which the modern type of dentition is derived by pushing the low and elongate upper dental plate further back in the mouth, and introducing a "premaxillary" or "vomerine" tooth in front of it. In all cases the lower dental plate is vertically deeper than the upper, and rises into a prominent beak anteriorly. It is also characterized by having a descending process at the symphysis, which is more accentuated in the fossil than in recent forms. This process bears a triangular groove or excavation on its inner face, the roughened surface of which indicates that it was occupied by cartilage, since there was no sutural union at the symphysis. That this was the case is self-evident, for the anterior beaks could not have closed outside the upper dental plates when the mouth was shut unless the lower ones were mutually separated by a slight interval.

In a recent communication by Jækel,¹ it is stated that "von

Jækel, O., Ueber *Ramphodus* etc., *Sitzungsber. Ges. naturf. Freunde*, Berlin, 1903, pp. 383-393.

der Zahnform und dem Gesamtgebiss von *Ptyctodus* wissen wir noch nichts genaueres," and it is thought that "vielleicht ist *Ptyctodus* schon ein echter Vertreter der sechszahnigen Holocephalen, . . . die wohl von den *Coccosteiden* abstammen mögen." This author's evident unfamiliarity with the *Ptyctodus* type of dentition is no doubt responsible for his confusion of the upper and lower dental plates of a species of *Rhynchodus* from the Upper Devonian of Wildungen, Waldeck, and for the impossible suggestion that the nasal capsules projected into the triangular incisions which occur in the descending process of the mandibular dental plates.

That which is commonly interpreted as the *lower* dental plate

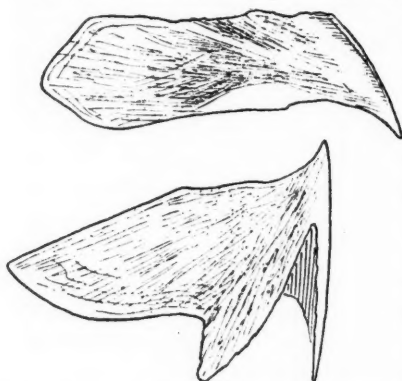


FIG. 1.—Left upper and lower dental plates (inner aspect) of *Rhynchodus major*, from the Upper Devonian of Wildungen (after Jaekel). $\times \frac{1}{2}$.

of *Rhynchodus*, Jaekel homologizes with the "premaxillary tooth" of *Chimæra*; and that attributed to the *upper* jaw of the former, Jaekel supposes to have functioned as a mandibular element. Referring to the lower dental plate from the Eifel Devonian described by F. v. Huene under the name of *Rhynchodus emigratus*, Jaekel states that he prefers to

regard it as a "Præmaxillarzahn," and notes its close resemblance to the Wildungen teeth called by him *Ramphodus tetradon*. So far as one may judge without having compared the original specimens, no essential differences exist between these forms and the earlier described *Rhynchodus major* and *R. rostratus*¹ respectively. An illustration of the Wildungen dental plates is given in the accompanying text-figure 1, slightly modified after Jaekel, that is to say, the latter's figure is inverted, and the upper dental plate is thrust forward so as to protrude beyond the lower.

¹ Eastman, C. R., Dentition of Devonian *Ptyctodontidae*. *Amer. Nat.* vol. XXXII, p. 487, 1898.—*Centralblatt für Mineral.*, 1900, p. 177.

RHYNCHODUS PERTENUIS, sp. nov.

Dental plate narrow and elongate, with sharp and extended cutting edge and knife-blade cross-section; anterior beak prominent, no symphyseal process, external surface smooth.

The unique dental plate upon which this species is founded was obtained from the Chemung of Franklin, in Delaware County, New York, and is preserved in the State Museum at Albany, where the attention of the writer was called to it by Dr. J. M. Clarke, State Palæontologist, but not in time to include its description with other fish remains already made known from the same locality.¹ The general outline and proportions of this form differ from those of all other species, and the absence of a symphyseal process is a very unusual feature. But for the trenchant cutting edge and narrow cross-section, the

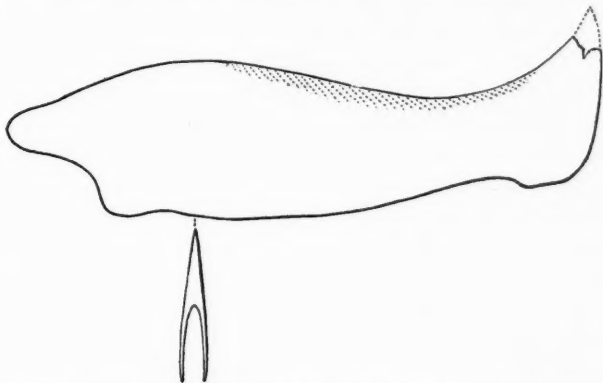


FIG. 2.—*Rhynchodus pertenuis*, sp. nov. Mandibular dental plate, $\times \frac{1}{2}$. Chemung group; Delaware County, New York.

specimen might be readily mistaken for a lower dental plate of *Ptyctodus*, instead of *Rhynchodus*. That it is properly a mandibular element, and referable to the latter genus, seems to admit of no question. The hollow along the base indicates the extent to which the plate was buried in the supporting cartilage of the jaws. The total length is 9 cm.

¹ *Ann. Rept. State Geol. N. Y.* 1897 (1899), pp. 317-327.

Fragments of chimæroid jaws have been previously reported from the Chemung of New York State by Clarke, but no specific identifications were attempted by him. At best this class of remains appears to be very rare in the eastern province, Ptyctodus and Rhynchodus being the only genera that are known from the New York Devonian. An undescribed species of the former occurs in the Corniferous limestone of Le Roy, and *P. calceolus* is apparently represented in the Hamilton stage at Eighteen Mile Creek, near Buffalo. Detached tritons from both of these localities are preserved in the Museum of Comparative Zoölogy at Cambridge.

ONCHOSAURUS Gervais.

Syn. Ischyrrhiza Leidy; Gigantichthys Dames.

A comparison of the type specimens of Gervais' *Onchosaurus radicalis*¹ and Leidy's *Ischyrrhiza antiqua*,² the former being preserved in the collection of the School of Mines at Paris, and the latter in the American Museum of Natural History in New York, leaves no room for doubt that they are generically, and probably also specifically identical, in which case Leidy's title must be abandoned. The original of Gervais' description, together with one or two duplicates, was derived from the Upper Cretaceous of Meudon, near Paris, and regarded through error as of mosasaur nature. The identical form occurs also in the Mæstricht Chalk, a remarkably fine specimen from this locality being preserved in the Paris Museum of Natural History.

The type of Leidy's genus, *I. mira*,³ was founded on a unique tooth from the Cretaceous Greensand of Burlington County, New Jersey, and supposed by the author to represent a Teleost fish related to Sphyræna. The original has never been figured,

¹ *Zoologie et Paléontologie Françaises*, vol. 1, p. 262, pl. lix. fig. 26, 1852.

² *Proc. Acad. Nat. Sci. Philad.* vol. VII, p. 256. 1856. — Emmons, E., *Report North Carolina Geol. Surv.*, p. 225, figs. 47, 48, 1858. — Leidy, J., in F. S. Holmes' *Post-Pliocene Fossils of South Carolina*, p. 120, pl. xxv, figs. 3-8. 1860.

³ *Proc. Acad. Nat. Sci. Philad.* vol. VII, p. 221. 1856.

and its present whereabouts are unknown. The so-called *Ischyrrhiza antiqua* is stated by Leidy to occur in New Jersey, North and South Carolina, New Mexico and Mississippi, but the differences between this and *I. mira* are inappreciable, and the two were finally pronounced identical by their author. Certain hypural fans similar to those accompanying Protosphyræna in the English Greensand have been theoretically associated with *Ischyrrhiza*, but with questionable propriety.¹ No reasons have been assigned for making this association, and other considerations militate against it, hence it appears advisable to exclude these fans altogether from the same genus.

The wide geographical distribution enjoyed by *Onchosaurus* is shown by its occurrence not only in Europe and America, but also in the Upper Cretaceous of Egypt. In 1887 a tooth differing from the type species only in unimportant particulars was described by Dames² from the Senonian of Gizeh under the name of *Titanichthys pharao*, the generic title being subsequently changed to *Gigantichthys*. Dames' figure was copied by Zittel in his "Handbuch",³ and the two authors agree in placing this form in the vicinity of *Enchodus*, although "*Ischyrrhiza*" is referred by Zittel in the same work to the *Esocidæ*. The latter position was first suggested by Cope, and is likewise adopted by O. P. Hay.⁴ It will be seen, therefore, that there is good authority for regarding *Onchosaurus* as one of the early fore-runners of the pikes.

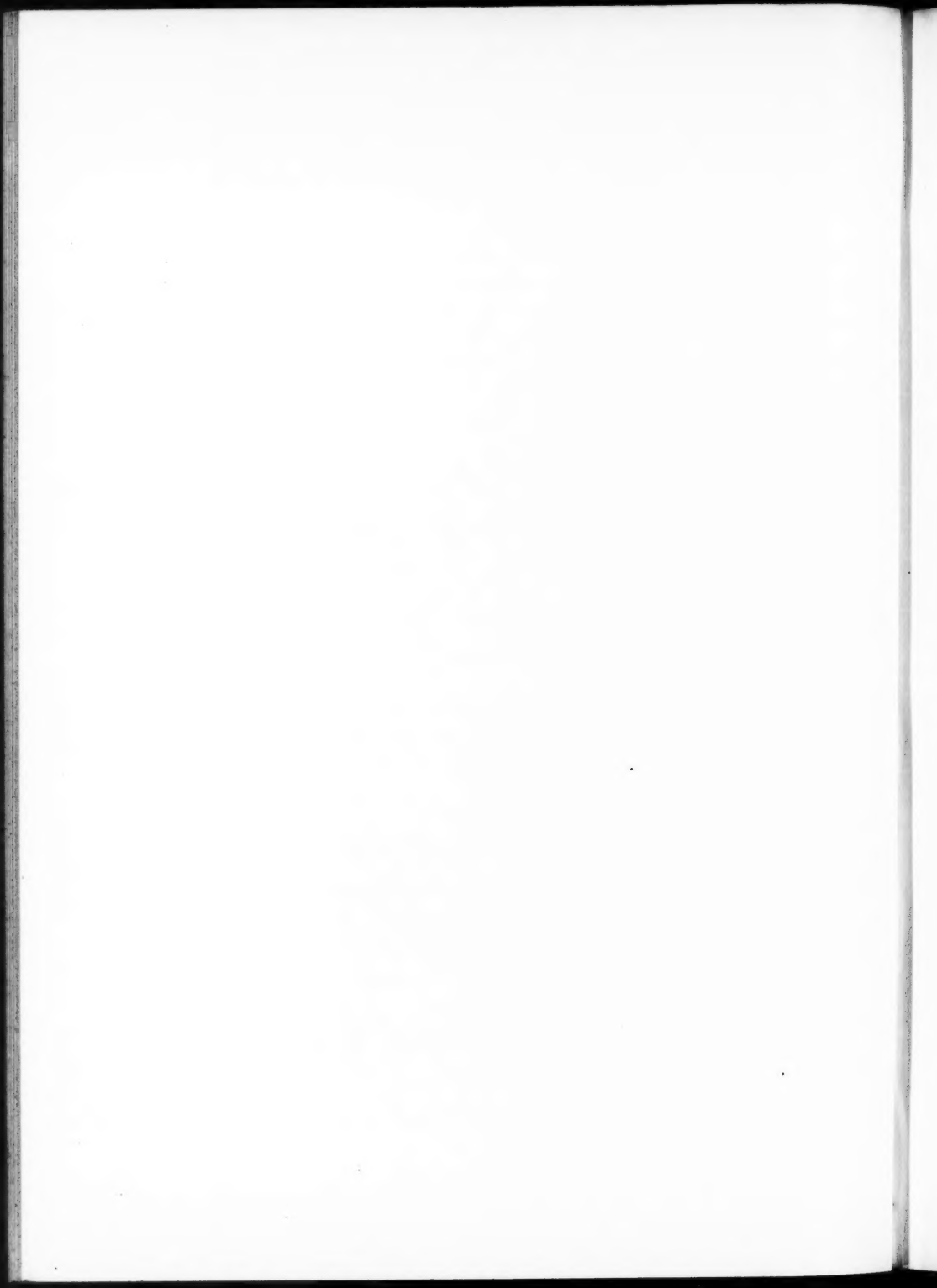
CAMBRIDGE, MASS.

¹ Cope, E. D., *Vertebrata of the Cretaceous Formations of the West*, p. 280. 1875.—Clark, W. B., *Bull. U. S. Geol. Surv.* no. 141, p. 60, pl. vii, fig. 2a. 1897.—*Maryland Geol. Surv., Eocene*, p. 112, pl. xii, fig. 8. 1901.

² *Sitzungsber. Ges. naturf. Freunde*, Berlin, p. 70, with figure, and p. 137. 1887.

³ *Handbuch der Paläontologie*, vol. III, p. 269, fig. 274. 1890.

⁴ *Bull. U. S. Geol. Surv.* no. 179, p. 398. 1902.



FURTHER INSTANCES OF PARIETAL DIVISION.

ALES HRDLICKA.

SINCE the publication of my monograph on "Division of the Parietal Bone in Man and other Mammals,"¹ there appeared in print three other direct or indirect communications on that same subject by Frassetto,² Schwalbe,³ and Le Double.⁴

The new instances of the anomaly reported by these authors are as follows:

A. In human adults.—1. An antero-posterior complete division of the left parietal in an "adult Savoyard" (Le Double);

2. A complete vertical division, "originating from the sagittal point" and "terminating in the inferior border" of the right parietal, in the skull of an adult male (Le Double). The race of the individual is not mentioned and the description leaves much in doubt.

3. A division in the right parietal of a "heavy, sclerotic," skull of a male Egyptian. The division runs from the coronal to the posterior third of the inferior border, and connects with a trace of a vertical division (Frassetto). As the author states that the usual sutures, even the parieto-temporal, are sinostosed, there is great uncertainty as to the character of the division; it suggests a traumatism more than an anomalous suture.

B. In human children and fetuses.—1. An antero-posterior complete division in the right parietal of a seven year old child, sex and race unknown. Skull hydrocephalic (Schwalbe).

2. An antero-posterior complete division in the left parietal

¹ *Bull. Amer. Mus. Nat. Hist.*, Vol. 19, Art. VIII, pp. 231-386, N. Y. July, 1903.

² Notes de Craniologie comparée, *Ann. sci. nat.*, pp. 148-187, September, 1903.

³ Ueber getheilte Scheitelbeine, *Zeitschr. Morph. Anthropol.* 1903, pp. 1-74, Stuttgart.

⁴ *Traité des variations des os du crâne de l'homme*, Paris, 1903, "Parietal," pp. 101-141.

of a new born child. Sex and race unknown. Skull hydrocephalic (Schwalbe).

3. An antero-posterior complete division in the right parietal in a female new born child (Frassetto).
4. An antero-posterior complete division in the right parietal of a six months' foetus. Sex and race not given (Frassetto).
5. An antero-posterior complete division in the right parietal



FIG. 1.—Anomalous division of the left parietal bone in a rachitic human foetus.

of a four to six months' foetus, sex and race not given (Frassetto).

6. A separation of the mastoid angle of the left parietal in an infant. Sex, age and race not given (Frassetto).

C. In Primates.—1. *Simia sabca* (Cercopithecus). Right parietal divided into four parts. This same case, apparently, is reported by both Frassetto and Le Double.¹

¹ Frassetto says the skull is No. A-1341 of the galleries of comparative anatomy of the Museum of Paris, while Le Double reports his specimen as No. A-134, in the Museum of Comparative Anatomy, Paris. Neither account is a thorough one.

2. A vertical, curving, complete suture in the left parietal of a young *Semnopithecus* (Frassetto).

3. A vertical, complete suture in the right parietal of a *Cercopithecus callitrichus* (Frassetto).

4. An oblique, vertical, complete, but synostosed suture in the right parietal of a *Macacus sinicus* (Frassetto).

5. A separation of the sphenoidal angle of the right parietal in a Mormon maimon (Frassetto).

D. *Other Mammals*.—1. *Ursus americanus*, young. The



FIG. 2.—Abnormalities of the right parietal in the rachitic human fœtus.

left parietal is divided into four irregular pieces. On the right is found a separation of the sphenoidal angle and an oblique, incomplete suture running downward and forward from the sagittal border near the lambda. This case, too, is reported independently and imperfectly by Frassetto and Le Double.

The new cases of complete parietal division that came to my attention since July, 1903, are briefly these:—

B. 1. A human foetus,¹ of white parents, born at term, ninth pregnancy. The child weighed three pounds and lived four days. Whole skeleton highly rachitic.

Both of the parietals, besides other bones of the skull, show considerable modification. (Figs. 1 and 2.)

The left parietal is divided into two by a narrow and somewhat irregular membranous space running antero-posteriorly, very nearly parallel with the line of the sagittal junction, which is also membranous. The upper portion is slightly higher than the lower, its maximum height, measured by a tape, being 4.2 cm., while that of the lower piece is 3.8 cm.

The anterior third of the dividing space is very wide, forming a large fontanel, and this is filled with one large and one smaller secondary bones. Posterior to the two portions of the parietal and between these and the occipital, from the sagittal line to the mastoid, is another space, in the mean 2.5 cm. broad, somewhat narrower inferiorly than superiorly, filled with various sized secondary ossicles.

The squamo-parietal junction and much of the fronto-parietal are still membranous.

On the right there is plainly but one parietal. This is comparatively small and somewhat irregular. In about the middle of the anterior border is a V shaped defect (fontanel), corresponding to that on the left, and filled with a moderate sized secondary bone. The whole fronto-parietal junction is occupied by a row of such bones and the same is true of the sagittal, parieto-occipital and to a less degree the squamo-parietal spaces. One of the secondary bones occupies the antero-superior angle of the parietal area and is of a large size, but is plainly of an accessory character, formed from an accidental accessory focus of ossification. Another larger bony piece occupies the asteric angle.

The skull has been somewhat deformed in preparation or drying and the posterior parietal region on each side is depressed, showing on this account but imperfectly in the illustrations. The bregma fontanel is large and partly filled with small sec-

¹ No. 9754, Army Med. Museum ; gift of Dr. M. D. Spackman.

ondary ossicles. The occipital bone shows the ordinary at this age separation of the squama, exoccipital and basal portions. The development of the temporal bones, particularly the squamæ, is much retarded.

This case is of interest in several ways. It is another instance where the anomaly of parietal division is associated with a pronounced pathological condition of the skull. Such association, particularly with hydrocephalus (some degree of which may have existed even in the skull under consideration), is so common in the children and foetal series of the cases reported that the causal relation of these pathological conditions with the divisions becomes more and more firmly established. They, of course, play the role of the exciting cause only, the fundamental condition which makes a parietal division possible being the presence of two starting foci or centers of ossification of the bone. In this connection one is forcibly reminded of the apparent rarity of pathological conditions in the adult human and also in the ape and monkey skulls with parietal divisions. Even if it be granted that much may right itself during the growth of the skull, it would seem that at least some of the parietal divisions in man and most of those in lower primates must be due to other exciting causes than rickets or hydrocephalus.

The second point of interest in the present case is the presence of two large and plainly *accessory* bones (antero-superiorly and postero-inferiorly on the right) which in an adult skull could easily be taken for primary portions of the parietal. As can be seen in the illustration the small true parietal on the right side shows a marked cleft near the middle of the anterior border. This cleft, it has been amply demonstrated before, is a remnant of the original membranous space between the upper and lower parietal centres. We had here, then, the two normal elementary foci of the bone and in the usual position. But the growth of the already fused primary parietal, due to rachitis, was retarded. Such a retardation in any of the bones of the cranial vault and from any reason leads invariably, undoubtedly through some trophic impulse which regulates the cranial growth, to the appearance of more or less numerous secondary foci of ossification, from which result various sized supple-

mentary, compensatory bones, commonly known as the wormians. Some of these secondary centres, as a rule those in localities where the greatest deficiencies exist, which is at the fontanels, show often more vital strength than others, enlarge to more striking dimensions and eventually, meeting and articulating with the advancing primary parietal, seem to represent and are mistaken for separated parts of this bone. There is no doubt but that the great majority of the "bregma," "human interparietal," and supraoccipital bones, as well as many of the "separated angles of the parietal" belong to this category. The difference between the compensatory bone and one that arose from lack of fusion of the primary centres is morphologically and particularly etiologically important.

The third point that the case at hand illustrates very handsomely is the possibility of a formation of a vertical parietal suture without any division, or totally independent of a division, of the primary parietal. Had the conditions in this skull advanced to a full development and particularly into adult life, before which period many of the closely packed wormians fuse, we should have had, unless an early synostosis obliterated the

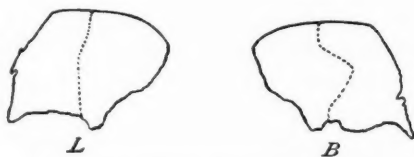


FIG. 3.—Bilateral, nearly obliterated vertical parietal division in a Hapale.

feature, a case very much like that of Fusari, which posess, I am inclined to think, falsely as an example of vertical parietal division in a human individual.

C. 1. Hapale, male, adolescent (No. 36,222, Dept. of Biology, U. S. Nat. Mus.). Skull apparently normal, symmetrical. The ordinary sutures all open. Each parietal shows a plain trace of a complete, vertical, now synostosed division. On the left the division began superiorly 9 mm. posterior to the bregma and 13 mm. anterior to the lambda, ran, slightly curving and nearly parallel to the coronal suture, to the temporal ridge, then

made a slight bend backward and ended a short distance anterior to the squamo-mastoid junction. The right division began one mm. posterior to that on the left and running a much more angular course terminated in the same relative position as that in the opposite parietal (Fig. 3).

2. *Cebus apella*, male, adolescent (No. 59,298, Dept. of Biol., U. S. N. M.). Skull slightly asymmetrical, surface of bones irregular (rachitis?). No injury. On the left side a serrated, vertical-oblique suture separates a large portion of the antero-inferior angle of the parietal. The anomalous suture begins anteriorly 10 mm. from the point where the coronal meets the fronto-malar suture (there is a bilateral malo-parietal articulation), and 36 mm. from the bregma; it ends inferiorly 14 mm. posterior to the meeting of the malo-parietal with the spheno-parietal suture and 51 mm. anterior to the asterion. On the right side 14 mm. above the point of meeting of the coronal and the frontal suture is a small v cleft in the parietal and from this runs backward and slightly downward a 4.5 mm. long fissure. On the same side exists a 13 mm. long, slightly wavy, vertical fissure in the frontal squama. It rises vertically from the fronto-

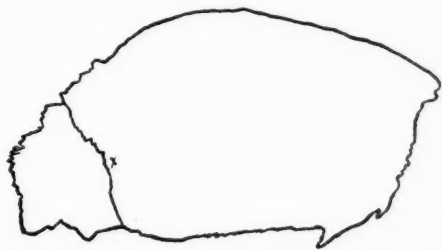


FIG. 4.—The left parietal of a *Cebus apella*, showing a separation of the antero-inferior angle.

malar suture and reaches the frontal part of the crest of the temporal muscle. There is no trace of any violence that might account for this fissure. (Fig. 4.)

The total number of ape, monkey, and lemur skulls examined in the U. S. National Museum was 316. A large majority of these skulls are those of adults, but no specimen was considered in which all the normal sutures of the cranial vault were not

plainly traceable. The varieties, and the parietal divisions found, are as follows :

- | | | |
|----|-------------------------------------|--------------|
| 11 | Lemurs | no division. |
| 6 | Galagos | " " |
| 1 | Tardigradus | " " |
| 11 | Propithecii | " " |
| 1 | Gorilla | " " |
| 1 | Orang | " " |
| 1 | Chimpanzee | " " |
| 11 | Gibbons | " " |
| 23 | Semnopithecii | " " |
| 27 | Presbytes | " " |
| 8 | <i>Simias concolor</i> | " " |
| 1 | <i>Nasalis larvatus</i> | " " |
| 1 | <i>Cynopithecus niger</i> | " " |
- 82 Macaques no division in 79; in one, from Siam (No. 83,274), there is in the right parietal above the sphenoidal angle a moderate size, curving, antero-posterior fissure; in one *M. rhesus* (No. 83,476), a vertical fissure runs on the left from the posterior third, on the right from the posterior fourth of the sagittal border towards near the middle of each parietal; in another, *M. rhesus* (No. 63,379), there is on the left parietal a trace of what was probably a complete vertical suture, running from the middle of the sagittal to the inferior border of the bone.
- 15 Cynocephali no division in 14; in one (No. 22,904), young, there is a partial vertical division in each parietal, left 10 mm. long and starting from between the anterior and middle thirds, right 19 mm. long and starting from between the third and last fourths of the sagittal border.
- | | | |
|---|---------------------|--------------|
| 1 | Colobus | no division. |
| 5 | Cercocebi | " " |
- 19 Cercopithecii no division in 18; in one (No. 36,277), there is in the right parietal a vertical-oblique fissure which begins superiorly between the anterior and middle thirds of the sagittal border and runs to the parietal eminence.
- 34 Cebi no division in 32; in one (No. 59,298, described in

- detail), a suture separates the left sphenoidal angle; in one (No. 82,779), there are two fissures, each 10 mm. long, in the superior third of the coronal border of the left parietal.
- 9 Hapale no division in 8; in one (No. 36,222, described in detail) a bilateral complete vertical division.
- 4 Midas no division.
- 1 Aotus " "
- 1 Brazil monkey No. 984, there is a 4 mm. long, vertical fissure in the superior border of the left parietal, slightly anterior to its middle.
- 7 Chrysothrix no division.
- 2 Lagothrix " "
- 10 Mycetes " "
- 4 Alonata " "
- 1 Nictipithecus rufipes " "
- 16 Ateles no division in 14; in one *A. geoffroyi* (No. 8,974), young, the left parietal shows two incisures, one horizontal, 10. mm. long, just above the lower third of the coronal border, and one vertical, 15 mm. long, running from the middle of the sagittal border. In one *A. ater* (No. 63,425), there is in each parietal, a short distance anterior to the middle of the superior border, a vertical, 9 mm. long fissure.

The main facts accentuated by the examination of this National Museum series of monkey skulls is the relative rarity of parietal divisions in adult specimens. The condition in all forms should be sought for preferably in the young. As a rule, synostosis is later at least in some, and at times in all, of the normal parietal articulations than in the abnormal divisions.

COMPARISON OF THE PROVISIONAL SCHEMES OF THE CLASSIFICATION OF BIRDS.¹

R. W. SHUFELDT.

It is not my intention in the present paper to offer any scheme of my own for the classification of birds, although it is a question that has long engaged my attention, and I hope soon to publish, in another connection, a provisional scheme, presenting what I take to be a natural taxonomy of Aves in so far as it is now understood. My only object here is to offer a few brief remarks upon the more prominent schemes for the classification of birds which have been put forward within recent times, and in a way compare the views of their sponsors. Careful recapitulation, undertaken from time to time, is always an advantage to any science, especially if that recapitulation is made along comparative lines and according to scientific methods. In other activities in which men engage, the benefits attaching to the occasional calling of a halt, with the view of taking account of the progress made; to making sure that advancement is being made along the right lines, has always been recognized. This, too, holds true in the domain of ornithological science. In fact, those who make the greatest, the surest and most substantial progress in anything are the ones who command a digested and available knowledge of all that has been previously accomplished in the field in which they labor.

It will be a red-letter day for our science when any species or subspecies of birds is and are known throughout the world by the same name, vernacular or scientific. That is, the opinion in regard to nomenclature will be unanimous. There will be equal rejoicing when that day arrives, when a unanimity of opinion exists in regard to the classification of birds. It is quite possible that many species now existing in the world's avi-

¹ Read by title at the twenty-first Congress of the American Ornithologists' Union, held at the Academy of Natural Sciences of Philadelphia, 1903.

fauna will, when that time comes, be extinct. With nomenclature I have nothing to do. Names are the inventions of men, whereas on the other hand, the relationships existing among birds in nature are actual, and in so far as invention enters here, it can only be in the form of printed, diagrammatic, or other device, to convey to the eye and mind what our conceptions of those relationships are. We may change names at any time and invent new ones *ad libitum*, but not so real relationships. These are fixed, and it remains for us to ascertain what they really are, and express them in the simplest terms. This is a matter of time, and I know of but two ways by means of which a consensus of opinion of ornithologists can be arrived at. First, by our mastering the morphology, geographical distribution, habits and life histories of all existing forms, and the osteology and other remains of all extinct ones within our ken; second, by the meeting of competent ornithologists in congress to discuss anything that touches upon the classification of the Class, and especially of the visible means of representing digested ideas in regard to it. Much could be accomplished by an international congress like the Second International Ornithological Congress which met at Budapest in 1891.

Of all the papers read at that Congress, none attracted more attention nor has been more useful or more closely studied since, than the paper read by Dr. R. Bowdler Sharpe, entitled "A Review of Recent Attempts to Classify Birds." It is the best thing of the kind extant and is so well known to ornithologists the world over as not to need further comment. I acknowledge with pleasure the assistance it has been to me in preparing the present paper. Apart from the many sound suggestions made by Dr. Sharpe in that address, and the historical lore it places at one's command, the main assistance I have derived from it has been the opportunity it affords me to study and to compare so many of the schemes of classification that have been proposed from time to time. To be sure, there now exist a number of other avian classifications. I refer especially to the classification of Aves proposed by Cope in 1889, entitled "Synopsis of the Families of Vertebrata," *The American Naturalist*, Vol. XXIII, pp. 849-877, and also to the taxonomic scheme brought forward by Gadow in

his contribution to the *Proceedings of the Zoölogical Society of London* for the year 1892, entitled "On the Classification of Birds," (pp. 229-256). So far as I am at present aware, Cope's and Gadow's classifications of Aves are the only two of any importance that have been published since Sharpe gave us his brochure cited above. If this be true, there has been no completed classification of this Class of Vertebrates published for over ten years. There have, however, been a number of such schemes partly completed and partly published, as for example the classification of birds as set forth in Sharpe's *Hand-List of Birds*, now passing through the press, and of which but one part remains to be issued. This admirable and most useful work will contain one of the most elaborate classifications of birds ever published. It is especially valuable inasmuch as Sharpe belongs to that school of ornithologists which believes in employing all available characters in classification, in ascertaining true affinities, to the end that the classification shall be a natural one and express as far as possible the real relationships of all existing families of birds, even to the minor divisions of species and varieties.

Within the past few years there have appeared some excellent summaries of classifications; for example, Ridgway's admirable presentation of the matter in his *Birds of North and Middle America*. "Nothing original is claimed for the classification here given," says its author, "except as to the form in which it is presented. It is simply the result of an elective process, the evidently good of other systems being retained and the obviously bad rejected, according to the author's ability to correctly interpret the evidence" (p. 6). In this connection I desire also to invite attention to the avian classification found in the *Catalogue of Osteological Specimens of the Museum of the Royal College of Surgeons of England* (Part III, Aves). This admirable piece of work is by Sharpe, who states that "The system of Classification followed in the present work is mainly that proposed by Henry Seebohm in his 'Classification of Birds,' and further elaborated in this 'Birds of the Japanese Empire.' There are some points in his system which I have slightly modified; but they are of minor importance when compared with the fact that every group of birds, as diagnosed by Seebohm, possesses a

combination of definite features, which are characteristic of the group, and of that group alone, be it Order or Suborder" (p. 1).

Finally, in many of the "Manuals" and "Keys" and "Hand-books" and "Check Lists" published in various countries, we have other classifications, but these, inasmuch as they do not enter upon the subject in its entirety, are apt to be more or less unsatisfactory and often misleading. The *Check-List of North American Birds*, prepared by a Committee of the American Ornithologists' Union" (Second and Revised Edition, 1895), is a very good example, for in it we find a classification that although it would be of great credit to a taxonomer of the Curvierian epoch, it certainly can now only be regarded in the light of a curious bit of antiquated literature which it would be difficult to fit into any modern taxonomy of the Class Aves published since the days of such worthy pioneers as Nitzsch, Illiger, and Müller. As cited above this classification appeared in 1895, yet in 1901 when Ridgway, who was a member of the aforesaid Committee responsible for the classification in the "A. O. U. Check-List," published his own taxonomic scheme the latter differed so markedly from the former that to compare them is quite like making a comparison of Wilson's old single-barrel, flint-lock gun with the finely finished modern double-barrelled, hammerless piece now in the hands of the present day ornithologist.

It would seem that we at least ought to be in position at the present time, or certainly in the very near future, to decide upon the main groups into which the Class Aves is naturally to be divided, yet such is by no means the case. This is the more remarkable, inasmuch as all the important part of the development of avian classification dates no further back than the one proposed by Huxley in 1867. This scheme belongs to the literature of the Darwinian epoch and was influenced by what was then known of the law of organic evolution, and consequently is the first scheme of classification worthy of our consideration. Huxley divided the Class into three orders, the Saururæ, the Ratitæ, and the Carinatae, and these three orders were divided into their suborders and certain groups.

Seven years later, or in 1874, appeared the well-known classi-

fication of Garrod, who it may be said, almost entirely ignored Huxley's scheme by dividing the Class Aves into two subclasses — the first containing four orders and the latter three, or in other words two sub-classes and seven orders as compared with the latter's three. Garrod's initial scheme of classification is not thorough since we meet with such incongruities as the Cathartidæ being considered simply as a group in the same order with the Steganopodes, herons and others, while the Columbidae and the Gallinæ are widely separated, and the penguins are placed as a family among the Anseres, immediately following the Anatidæ, or the ducks, geese, swans and their allies. Still keeping before us, however, the main divisions of the class it is to be noted that ornithologists had little more than fairly grasped the Garrodian idea of avian relationships when in 1880, six years after its publication, Sclater proposed another scheme. In it the Saururæ of Huxley are not considered, — the class is divided into two subclasses, the Carnatæ and Ratitæ, the former containing no fewer than twenty-three orders, and the latter three others, or twenty-six orders of birds, where Huxley only recognized three; and these three orders Newton considers to be so many sub-classes, while he would divide the Ratitæ into no fewer than six orders. These classifications were almost immediately followed by Reichenow in 1882 who divided birds into seven main groups which he called series, and these seven series were represented by seventeen orders. It is very different indeed from any of the foregoing schemes and cannot be contrasted with them without great difficulty, while its chief interest lies in the fact that he published in connection with it a phylogenetic tree of the Class Aves, one of the first attempts of the kind employed in ornithological science.

Within the next ten years a number of important classifications followed, — all provisional schemes for the arrangement of the Class, but none the less entitled to our best consideration, coming as they have from the pens of the ablest living ornithologists.

Stejneger's appeared in 1885; Fürbringer's in 1888; Cope's in 1889; Seebohm's in 1890; Sharpe's in 1891; and Gadow's in 1892. Of all these Fürbringer's is the most elaborate and

exhaustive, being accompanied by several vertical aspects and horizontal projections of his phylogenetic tree. Indeed, the objection brought against Furbringer's classification, principally by Gadow, is that it is too long and too elaborate for practical use. I do not fully concur in this opinion; moreover its author has, in many groups carried us a long way on the road toward determining the true relationships of birds and that, I take it, is the real goal we seek. In fact the converse of this would be an easy matter, that is to create a brief, artificial classification of birds based upon our present knowledge of the class, and adapted to the practical ends of the science. Any international congress of ornithologists, representatives from all parts of the world, could, in a few days, prepare such a scheme. But the problem is not to be settled in any such manner.

As it is we find hardly any more uniformity with respect to the schemes proposed by Stejneger, Fürbringer, Cope, Seebohm, Sharpe and Gadow, than is to be found among those of Huxley, Newton, Garrod, Forbes, Sclater, Reichenow, and others.

The majority of these schemes carry the classification down through the families, and, in special cases, in a few instances in each, through the sub-families. Huxley did not give the number of families in the Passeres, Garrod omitted the group entirely in his scheme; Sclater enumerated thirty-one of them; Reichenow but twenty-one; Stejneger thirty-three; Fürbringer reduced the typical Passeres to one single family, the *Passeridæ*; in 1889 the present writer recognized twenty families of the North American Passeres, and Sharpe the following year practically adopting the scheme, included all the old world representatives, and by so doing admitted thirty-five families as making up the passerine group,—and so on.

There is little need of carrying such comparisons as these into the higher divisions into which birds have been divided. We would but meet with greater variance of opinions, made the more deplorable from the fact that the wealth of coinage in new names renders the comparisons instituted even more perplexing. Then this perplexity is in no way diminished when a taxonomer takes it into his head to incorporate all the known fossil forms of birds into his scheme, as quite a number have done, and, very properly so.

It may naturally be asked, what are some of the chief reasons why the classifiers of this group of vertebrates do not exhibit a greater unanimity — a fact more remarkable when we come to consider that a dozen or more of those classifications coming from the pens of competent ornithologists appeared all within a very few years of each other. It is certainly not due to the fact that it has been demonstrated that birds have arisen from a prehistoric and extremely ancient stock of animals in common with the Reptilia, for knowledge of this character ought to have the tendency to harmonize views and opinions rather than to introduce the element of disagreement among them. We may eliminate too, I think, any difficulty that has arisen from the discovery of the few fossil forms of birds we have come in possession of, for many of these belong to the minor groups of existing birds, while others are not calculated to disturb a natural classification. Indeed, in some instances, they shed light on the subject. Again, in that existing birds are so completely differentiated from all other classes of animals now living upon the surface of the earth, ought to make them the easier to classify. They alone possess feathers and this establishes a line of demarcation for them, standing between the group and the nearest mammals or reptiles, quite as clearly defined as the possession of a mainspring separates all modern watches from an hourglass. The problem then presents itself in this wise, — to ascertain the true relationships both near and remote existing among all living birds, and then prepare as simple a scheme as possible expressing these relationships in terms that shall be in harmony with the classification schemes adopted in the cases of other classes of animals. In doing this, one of the first difficulties to arise is the marked homogeneity of the group. It is like classifying so many thousands of black, leather-covered hand cameras; they all look a good deal alike on their outsides, and the task would be equally difficult were we not permitted to examine into their interiors and ascertain the differences in their other parts, as the different kinds of lenses, finders, shutters, and other contrivances. Exactly the same thing obtains with birds. The great variance of opinions in the premises at the outstart is due to the difference in the amount of knowledge possessed by the different classifiers, especially as

to the characters presented on the part of the insides of the objects they are attempting to classify, although in saying this I do not underrate the value of the external characters.

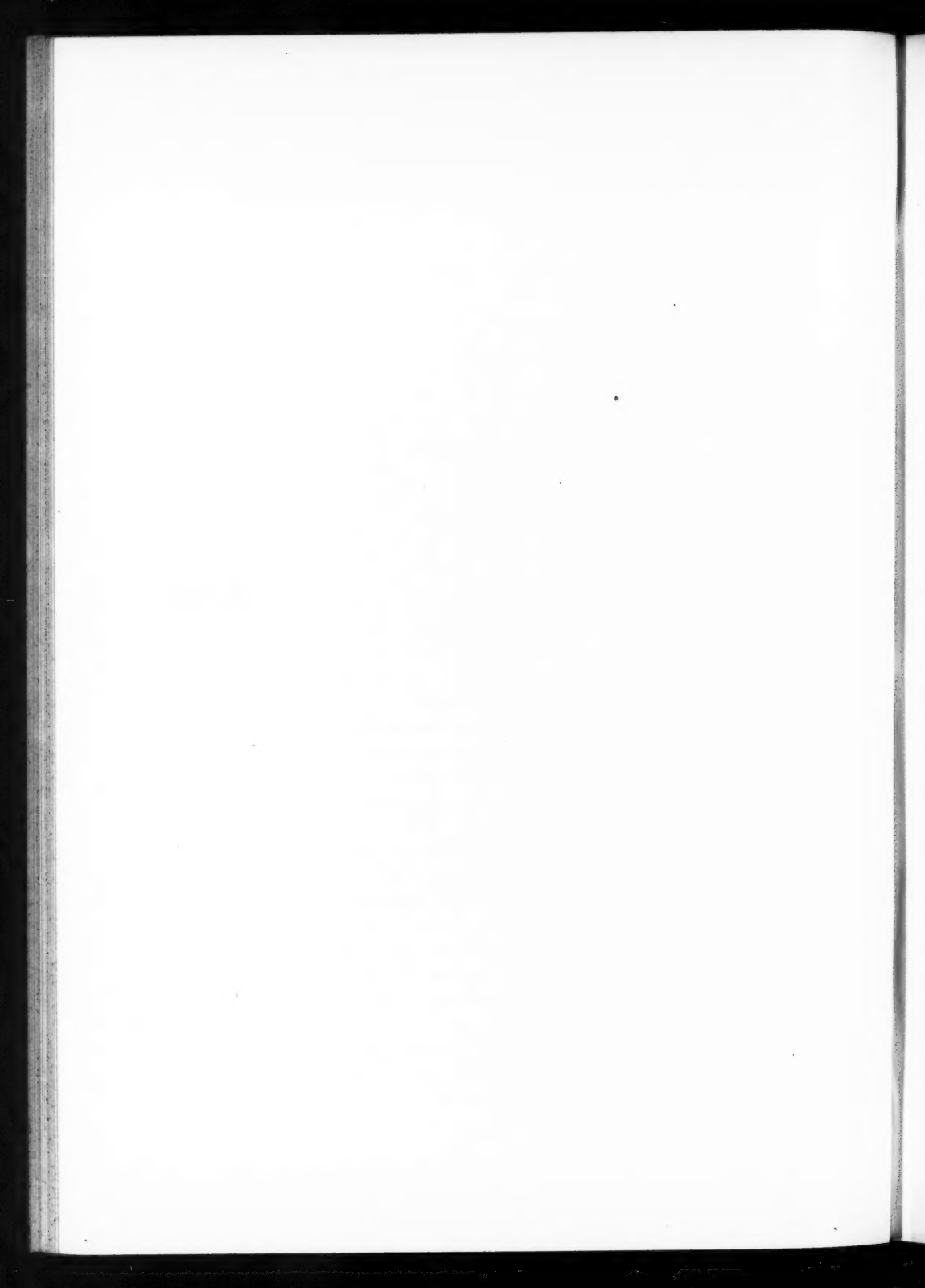
The facts, then, that birds are a very homogeneous group and the knowledge of all their characters possessed by individuals who have attempted to classify them, has differed very widely in amount, is the first factor that will account for the great differences to be seen in the various published classificatory schemes. These are not the only reasons, however, and another very obvious one is the attempt made by some classifiers to ignore the homogeneity of birds, and to arrange them after the manner of the other great groups of animals, such as mammals or fishes. In other words, the attempt is made to employ the same divisional groupings from subspecies to class in the case of birds, where perhaps no greater differences can be found than exist between a thrush and an ostrich, as they do in the case of mammals, where such gaps exist as the one separating man and the *ornithorhynchus*. The objection is raised here at once, however, that an order of birds, for example, is a very different thing from an order of mammals. This is a knotty question, and as time forbids my discussing it here, I can only say that it leads directly to another very obvious reason for the differences seen in the various arrangements that have been proposed for birds, and that is this: — although ornithologists, in this country at least, may be pretty well agreed as to what is meant by a species, it is not clear that the same apparent unanimity of opinion exists among them in regard to what is meant by a genus, or rather what constitute generic characters; and so on for families, suborders and other groups, until we arrive at the Class, and perhaps the Subclass, — groups, for evident reasons, again understood to possess the same value in all avian schemes of classification wherein they have been employed. The difficulty here is, no uniform laws have been drawn up setting forth for birds exactly what characters constitute specific characters, what generic characters, family characters, and so on up to Class characters. The consequence is that one avian classifier will employ subclasses in his scheme, which subclasses are designated in the scheme of another as super orders, or even as orders or some other divisional value in the scheme of a third

taxonomer, and so on for all those who have engaged in this difficult subject.

Finally, there is the great question upon which no two ornithologists now entertain similar opinions, and that is upon the various relationships of birds. Both this and the former question, however, depend entirely upon the amount of knowledge on the subject possessed by any particular taxonomer. The more exact and far-reaching this is, the nearer and sooner will he arrive at the truth.

In any event, it is very clear to me that the day is still far away when ornithologists will be agreed in reference to all these points. It is purely a matter of evolution, of development, and the acquirement of the necessary knowledge. Guess work will never attain the desired end, nor will any one man settle it. It seems to me, however, that we are in a position to discuss and settle one class of questions, that is in the case of birds, what groups shall be adopted in their classification, and what characters in birds themselves shall stand for those groups. For the rest the larger part of it depends upon substantially adding to our present knowledge of the morphology of these forms in its widest sense, and this to be supplemented by a very general knowledge of the entire life histories of all existing birds. From the very nature of things the latter advances with far greater rapidity than does the former, and we stand in great need of the addition of many more laborers in the fields of avian morphology. Death has materially thinned the ranks of this part of our army within a comparatively short space of time, and it has been principally the great captains of whom we have been deprived, — and we have by no means rallied from the loss of such workers in the anatomy of birds as Huxley, two of the Parkers, Gegenbaur, Garrod, Forbes, and other men of their calibre, power and influence, any one of whom would have said that the solution of the classification of birds lies in our commanding a knowledge of their history and structure.

NEW YORK CITY.



NOTES AND LITERATURE.

GENERAL BIOLOGY.

A Well Balanced Book on Theoretical Evolution.¹ — It seems to be generally agreed that we are beginning a new era in the study of Evolution; an era in which analytic and experimental methods will replace that of sharp logic. But the experimentalist works blindly without hypotheses and these the speculative writings have provided. It is a useful thing, at the beginning of this new era to have these hypotheses brought together by a broad-minded investigator; and this is the very arduous task that Plate has well done.

The immediate purpose of the work has been to stem the tide away from Darwinism, to show that whatever limitations the theory of natural selection may have as a complete theory of the origin of species it remains the only satisfactory theory of adaptation. The book, which is much increased in size over the first edition, is divided into five chapters. The first deals with the objections, less or more serious, that have been raised against Darwinism in the strict sense; the second with the different forms of selection and elimination; the third with the complementary theories; the fourth with the basic elements of evolution from which the theory of selection starts, namely, excess of births, variability, and means of isolation; the fifth with the range of applicability of the Darwinian and the Lamarckian factors. Then follow a Bibliography of over 10 pages and a good index.

The book is exceedingly satisfactory in most particulars. It is refreshing to find an author who does not insist that there is only *one* method of evolution. "Das Problem der Artbildung" he says, page 228, "darf nicht einseitig behandelt werden, weder ausschliesslich von Lamarck'schen noch vom selectionistischen Standpunkte; nur die Vereinigung beider Principien führt zum Ziele." Naturally the author does not follow Weismann in rejecting the inheritance of acquired characters and he is quite ready to accept the possibility of

¹ Plate, L. *Ueber die Bedeutung des Darwin'schen Selectionsprincipis und Probleme der Artbildung*. Zweite, vermehrte Auflage. Leipzig: Engelmann, 1903. 247 pp.

orthogenesis. In this breadth of view Plate doubtless approaches nearer to the spirit of the great master than the Neo-Darwinians. Nevertheless, in so far as a criticism may be aimed at the book it concerns Plate's unwillingness to accept more freely some of the other subsidiary or alternative theories that have been proposed. Thus the reviewer thinks that Plate does scant justice to the claims of the mutation theory; and in his discussion of means of isolation he entirely fails to mention Mendel's law of the segregation of parental qualities in the germ cells of mongrels. Nevertheless, this law must be an important factor in preventing the swamping of mutations. In his account of the different theories to explain organic adaptation there is not included the theory proposed by the reviewer and later by T. H. Morgan that there has been a selection by the organism of the environment for which its structure is fitted — but as the preface date is antecedent to the appearance of that theory such conclusion could hardly be expected.

This brief review can give no adequate idea of the scope, soundness and helpfulness of the book. It is recommended to biologists as by far the best on the subject.

C. B. D.

Experiments in Heredity.¹— Stimulated by the rediscovery of Mendel's Law of crossing, Bateson and Saunders have thrown together the results of their studies on crossing plants and poultry. As this is the first extensive post-Mendelian account of hybridization experiments in animals it may fairly be called epoch-making.

Miss Saunders worked with two hairy species of *Lychnis* and also a glabrous variety; with two varieties of *Atropa*; two species, each with two varieties, of *Datura*; and various races of *Matthiola*. In the first cross the hairy character is dominant and the glabrous recessive, as shown by the fact that all the first crosses were hairy. In the second generation, however, both dominant and recessive forms appeared in Mendelian proportions.

The *Atropa* experiments were less complete, but appeared to be Mendelian, showing dominance in the first color of the type form. The *Datura* experiments, involving 12 characters, were much more complex. Also there were exceptions to Mendelism in some cases, although striking adherence to it in others. Finally, the *Matthiola* experiments were based on so many races mixed together that the

¹ Bateson, W. and Miss E. R. Saunders. *Report I to the Evolution Committee, Royal Society, London*: Harrison & Sons, St. Martin's Lane, 1902. 160 pp.

results are hard to follow ; some were clearly Mendelian, others clearly not ; and some of these aberrant cases seem to be examples of what Millardet has called "false hybridism" — where the second and subsequent filial generations show no trace of one of the parents.

The poultry experiments were made with Indian Game, White Leghorns, Brown Leghorns, White Dorking, and White Wyandotte. The pea comb and single comb when crossed followed Mendel's law, the pea being dominant. The extra (Dorking) and normal toe followed the law approximately, the extra toe being dominant. In other cases the results were non-Mendelian. Thus it may happen that when a usually dominant character is crossed with a pure recessive the first filial generation is not purely dominant, but a mixture of dominants and recessives. It appears that a usually recessive character may sometimes dominate. The mixed result in the first filial generation may also be due to the fact that the "dominant" used in the cross was not a pure bred dominant but gave off "recessive" gametes.

The last 35 pages of the work are devoted to an invaluable discussion of "The Facts of Heredity in the Light of Mendel's Discovery." Here some new terms are introduced. In experiments in hybridization two forms exhibiting antagonistic characters are crossed. There may be one pair or many pairs of these antagonistic qualities. The antagonistic qualities are called allelomorphs. The zygote produced by the union of gametes with allelomorphs is called a *heterozygote* to distinguish it from a zygote formed of similar gametes (*homozygote*). Allelomorphs may be either simple like hairiness or smoothness ; or they may be compound, as the variegated color of some flowers. When a compound allelomorph is crossed with a simple the second filial generation may show not two forms only but several — the compound allelomorph has broken up into its constituents.

The relation of Mendel's Law to "skipping a generation," to prepotency, to sex (since elaborated by Castle) and to Galton's Law are discussed. The whole work closes with an eloquent "outlook" over the future of experimental breeding.

C. B. D.

Walks in New England¹ is a series of lay sermons which appeared in the Springfield Republican a year or two ago ; they are the records

¹ Whiting, C. G. *Walks in New England*, with illustrations from photographs. London and New York, John Lane. 8vo., pp. 301, 24 illustrations.

of a saunterer among New England's woods and fields. They record the aspects of the changing seasons from March to December with eyes which, in turn, are those of a lover of plants and birds, a poet, and a deeply religious man. For science he cares little, as compared with "the intuition of spirit"; Emerson and Whitman are more to him than Darwin and Wallace. The letters are not full of accurate detail like Thoreau, nor of vivid coloring like Bolles; the style is often too involved and the thought too mystical to suggest comparison with Burroughs; but coming as they did from week to week, they must have been very welcome to many who could not share the author's rambles; they breathe the calmness, the toleration, the kindly sympathy of a true lover of out-door nature.

ZOOLOGY.

Influence of Man on the Distribution of Reptiles and Mammals in Patagonia and Fuegia.—In a very complimentary review¹ of my recently published *Narrative of the Princeton Patagonia Expeditions*, Mr. Barnum Brown, who, as a representative of the American Museum of Natural History in New York accompanied me on my last expedition to that country remarks that my "observations on lizards should have been confined to that part of Patagonia north of the Rio Santa Cruz, for this river forms the natural southern boundary line for lizards as well as armadillos though a few have been scattered south of it by man." I have taken these small reptiles at Fitzroy's Springs on the north shore of the Gallegos river, at various points along the coast between Cape Fairweather and Coy Inlet, about the Salt lagoons at the estancia of Montes and Fernandez ten miles from Gallegos, at the Mount of Observation and at Greenwood's estancia sixty miles south of Santa Cruz and have observed them at many other favorable localities in the region south of the Santa Cruz River, while other travellers have reported them as being common not only in this region but on the *plains* of Fuegia as well. See Popper's account of Fuegia in Mulhall's *Hand-Book of the River Plate*. I see no good reason for attributing the present wide distribution of these lizards over the region south of the Santa Cruz River to the agency of man.

¹*Amer. Nat.*, Nov. 1903, pp. 799-800.

Mr. Brown's remark that the presence of the guanaco in Fuegia while the deer, rhea and puma are absent from that island is attributable to the agency of man rather than to the superior powers of self-distribution possessed by the guanaco, may be correct, but the latter hypothesis seems to me the more reasonable one. If the presence of the guanaco in Fuegia is due to the agency of man, why is the rhea absent from that island? It is found quite as often in captivity among the Indians, could have been just as readily transported and is more prolific than the guanaco. The readiness with which the guanaco takes to water is well known in Patagonia as are also its powers of swimming and to these characters is due I believe its presence in Fuegia. The absence of the deer in Fuegia which, as is well known, is also a ready swimmer is I think due to the fact that it is a forest and mountain species and does not advance on the plains as far as the "narrows" of the Magellan Straits. Farther west the channels between Fuegia and the mainland are too wide to be successfully crossed by either the deer or guanaco.

J. B. HATCHER.

The Rat-tailed Rotifers.¹—Jennings has published a most interesting and valuable monograph of the Rattulid Rotifers, which although a part of a series entitled "Rotatoria of the United States," actually includes the species of the whole world. In fact, one new species described (*Diurella dixon-nuttalli*) has never yet been found in America but only in England. The species are divided into two genera; *Diurella* in which the two caudal appendages or toes are equal or the shorter is more than a third the length of the longer, and *Rattulus*, in which these organs are more unequal, one being often quite rudimentary. The author states that these are not natural genera, but are justified by considerations of convenience. He remarks that the idea that all the species of a genus must be more related to each other than to any outside species has been largely given up in practice; but this might be admitted and yet it might remain true that the generic characters had not been acquired independently. If the more primitive *Diurella* type has given rise separately to two or more groups of species now included in *Rattulus*, it will be necessary to either divide *Rattulus* into as many genera, or unite *Diurella* and *Rattulus* under the latter (older) name. Of

¹ Jennings, H. S. A Monograph of the Rattulidæ. *Bulletin U. S. Fish Commission* for 1902 (1903). pp. 273-352. Pls. I-XV.

course it may be impossible to demonstrate this, in which case the present classification may very well be allowed to remain. The genus *Heterognathus*, Schmarda, is applicable to the species having the toes equal—part of the present *Diurella*. The author admits that this group may be thought worthy of separation, but he does not notice that the name belongs properly to a genus of fishes, the latter having five years' priority. If the equal-toed species deserve a generic name, a new one will have to be proposed.

Looking over the paper, one notices the absence of any records from the region west of the great plains, as well as from other great regions. It is to be hoped that students will arise in some of the neglected parts of the country, now that the study is made comparatively easy.

T. D. A. C.

Gardiner's Reports on the Fauna and Geography of the Maldive and Laccadive Archipelagoes have now begun a second volume. The First Part contains an account of the Alcyonaria, by Hickson and E. M. Pratt, of the nudibranchs by Sir Charles Eliot, of Sponge crabs by Borradaile, of Lagoon Deposits by Gardiner and on a Land Planarian by Laidlaw. The Part contains nine lithographed plates.

Hickson discusses the remarkable variability of the Alcyonaria and concludes that either they constitute a large number of closely similar species or else one species capable of extraordinary variation in circumstances that are approximately identical. For practical purposes the author regards those variations as species which are discontinuous. Hickson finds that the form and mode of branching are unreliable criteria of any species because they vary with accidental variations in environment and the presence of gall producing Crustacea that reside in the branches.

Eliot's Report contains many interesting general data, concerning swimming Hexabranchiæ, hidden but highly colored Dorididæ, self-mutilating Dicodoris, a Phyllid that secretes a liquid with disagreeable smell and others.

C. B. D.

Position of the Gordiacea.—Montgomery concludes¹ from a study of the adults that the Gordiacea agree with the Nematoda in only the tubular genitalia and their opening into the cloaca. They

¹ *Zoolog. Jahrbücher* Abth. f. anat. xviii 1903.

agree with the Annelids in structure and innervation of the muscles and in dorso-ventral mesenteries bounded by epithelia. They differ from Annelids in entire absence of true metamerism, in the absence of a prestonial ganglion, in absence of seton and appendages and in structure of genitalia. The group cannot be regarded as degenerate Annelids (Vejdovsky) or as modified Nematods, but must be considered as an isolated group (Funacher, von Siebold, Villot) until more details concerning the development are known. The pertinence of the peculiar genus *Nectoruma* to the group is at least questionable.

North Atlantic Invertebrata.—Several papers in the 1st Hefts of the *Bergens Museums Aarbog* for 1903 have an interest to students of the Invertebrata of our northeastern coast. Emily Amesen catalogues the Sponges of the Norwegian coast, the present paper containing the Halichondrina. R. C. Punnett enumerates the Nemertini of Norway in which thirty-four species are recognized, of which twelve are supposed to be new. Edward T. Browne reports upon a collection of nineteen species of Medusæ, mostly from the fiords around Bergen, four of them being new and eleven others not previously catalogued from Norway. Among the interesting points brought out is the fact that the peculiar sucking cups described by Hæckel in *Ptychogastria polaris* (*Pectyllis arctica* Hæckel) are only the stumps of broken off tentacles. Only four species of Leptomedusæ are enumerated in the collection. All three papers are well illustrated.

BOTANY.

The Desert Botanical Laboratory.¹—Of the occurrences of recent date interesting to the botanists of this and other countries, one of great importance is the establishment, by the Carnegie Institution, of a laboratory at which desert plants can be studied in their native habitat. Messrs. Coville and MacDougal were asked to constitute themselves a committee of inquiry, to determine the most suitable place where such a laboratory might be located. We have before us

¹ Coville, F. V. and MacDougal, D. T. Desert Botanical Laboratory of the Carnegie Institution. pp. 1-58, Pl. I-XXIX, fig. in text 1-4. Publication No. 6, Carnegie Institution of Washington, Nov. 1903.

the report of their journey, undertaken early last year, which took them over most of the desert regions of the western part of this continent. The place decided on for the laboratory was a site about two miles from Tucson, Arizona, and since then the laboratory has been built and equipped. Besides the fact that the country around Tucson is of a distinctly desert type and the flora as varied as such a flora is apt to be, the practical questions of accessibility and of habitability were considered. With the two authors as advisory board, Dr. W. A. Cannon was appointed resident investigator and is at present engaged on various researches. Arrangements have also been made so that a limited number of trained investigators may avail themselves of the privileges of the laboratory. "Not the least important part of the duties of the resident investigator will be to aid visiting botanists and others."

This contribution besides containing a description of the trip undertaken for the purpose of selecting a site for the laboratory, also includes an account of the general botanical and climatic features of the deserts of the regions visited. While the two authors had both separately made trips to many of the same districts of the west, the itinerary of their present journey included almost all of the arid regions of the United States and of northern Mexico. Starting at El Paso they first made their way down to the sand dunes of Chihuahua, south of Samalayuca in Mexico. The winter vegetation of these siliceous sand hills is scanty, only a few forms are mentioned. The next point of attack was the Tularosa desert lying westward of Alamogordo, New Mexico, the most interesting feature of which is the region known as the White Sands, composed of drifting sand that is almost wholly gypsum. The characteristic plant of the dunes is *Rhus trilobata*, the roots of which bind the sand so effectually that clumps of the plant bring about the formation of pillars of sand when the surrounding dunes shift. A curious relation of plants of *Yucca radiosa* to the dunes was also noticed. Investigation showed that a *Yucca* growing out of the top of a thirty-foot dune, must penetrate with its trunk to the bottom. On excavating it appeared that the plant must have grown as the dune engulfed it. In the bottoms among the dunes the vegetation is much denser, a grass is plentiful and *Ephedra* is frequently met with.

Tucson was next visited, there the woody vegetation of the desert consists mainly of the creosote bush, the mesquite, joint pine, and several Cactus forms, while higher on the foot hills occur the giant *Cereus*, and species of the tree known as the palo verde. At the

time of the rains a variety of annual vegetation may spring up. From Tucson the authors proceeded to the Sonora region of Mexico, stopping at Nogales, and thence to Torres. Various interesting forms are described from this region, among the most remarkable of which is a cucurbitaceous tendril bearing plant, *Ibervillea sonorae*, whose root and stem base are enormously swollen for water storage, and a tree-like morning-glory (*Ipomoea arborescens*), which grows twenty to thirty feet high. At Guaymas on the Gulf of California, a curious mixture of plant forms was observed, the beach is lined with mangroves, while close to them were the strictly xerophytic Cacti, for as far as rainfall is concerned Guaymas is even more arid than Torres.

In the Colorado desert of California several types of vegetation are found, due to differences in the soils; there are the gravel hills, the alkali, and salt flats, the two last named showing a very restricted growth of vegetation. The fan-leaved palm, *Neowashingtonia filifera* is native to the eastern foot hills of the San Bernardino mountains which lie in the Colorado desert district. They grow in groves forming miniature oases where a clayey soil, from which oozes what water has come from the hills, crops out to the surface. Northward lies the Mohave desert where grows *Yucca arborescens* and *Juniperus californica*, while in the lower altitudes the creosote bush (*Covillea tridentata*), is the prevailing woody plant. From the Mohave the authors proceeded to the grand canyon of the Colorado, but were disappointed to find that the number of woody desert plants found along the canyon's sides were comparatively small. This they ascribe to the narrowness of the canyon which probably induces abnormal climatic conditions.

Following the account of the actual journey is a consideration of the characteristics of deserts in general and of North American deserts in particular. Meteorological tables are given, showing the rain-fall for various localities from Oregon, to San Luis Potosi in Mexico. One table of especial interest gives the mean annual precipitation as compared with the estimated annual evaporation. The ratio in favor of the evaporation is anywhere from 6 : 1 to 35.2 : 1. It is also pointed out that the distribution of rain-fall during the year is of great importance in determining the character of the flora. Another factor in the production of desert conditions which cannot be disregarded is the soil constituents, a fact that is illustrated by the conditions which exist in the gypsum containing White Sands of Tularosa, the "white alkali" which is mainly sodium sulphate and the "black alkali" where sodium chloride and sodium bicarbonate are the chief soluble constituents.

Historically the desert regions of North America are of interest, that area which was known as "the great American Desert" by cartographers as late as 1843, does not really exist as such. The deserts of this continent may be designated as the Sierra-Nevada desert, comprising portions of Utah, Idaho, Washington, Oregon, Nevada, California, Arizona, Baja California, Sonora, and Sinaloa; and the Chihuahuahua desert, which occupies the tableland of Mexico east of the Sierra Madre and north into Texas, Arizona, and New Mexico. It is further stated that for the purposes of this paper the desert lands of the Dakotas, of Montana and Wyoming may be considered as the extreme northern arm of the last named region.

As the closing section of the paper there is a discussion of the results of experiments by one of the authors, carried on at an earlier date. A comparison of two desert types, *Mentzelia pumila*, and an *Artemisia*, with two moisture loving forms, tomato and *Eucalyptus globosus*, shows that even in their natural habitats, where the conditions for transpiration are of course vastly in favor of the desert plants, the disparity between the water evaporation of the two is very great. As to temperature it was found that the plant-body of an *Opuntia* gave a maximum in the forenoon of as much as 111.2° Fahr., while in specimens of *Cereus* temperatures of 113° to 115° Fahr., were frequently found. The fact that this is above the critical temperature usually given for chlorophyll leads to the authors' suggestion that the protoplasm and the chloroplasts may have undergone changes which adapt them for such conditions, although, they add, it is not unlikely that the death of plants in such regions is as often the result of too great insolation as of lack of water.

The authors make no claim that their narrative is an exhaustive account of the regions visited, which considering the short time spent would of course be quite impossible, but express a hope that it will serve to show the great diversity which exists in the several floras which go to make up our desert flora as a whole. In this they can certainly feel that they have succeeded both in the text and in the admirable illustrations which are profusely scattered through the pamphlet. To any intending student of the conditions which exist in our deserts it is bound to be of great service and the full bibliography by W. A. Cannon which is appended will be an additional aid. This is the first publication relative to the desert laboratory, we may hope that many more will emanate from this source.

H. M. R.

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